BOTANICAL GAZETTE

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THE BOTANICAL GAZETTE

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P. 17, line 16 from above, for Weisner read Wiesner.
P. 61, No. 34, for Wurzelnspitze read Wurzelspitze.
P. 83, line 11 from above, for nucleus read nucleolus.
P. 89, line 18 from above, for adundant read abundant.
P. 91, line 20 from above, for cytolasm read cytoplasm.
P. 108, line 16 from below, for **26** read **27**.
P. 115, line 7 from above, for soons read soon.
P. 121, line 13 from above, for *plate V* read *plate IX.*
P. 126, second line from bottom, for periblem, terminal read periblem-terminal.
P. 135, lines 12 and 15 from above, for *des* read *de.*

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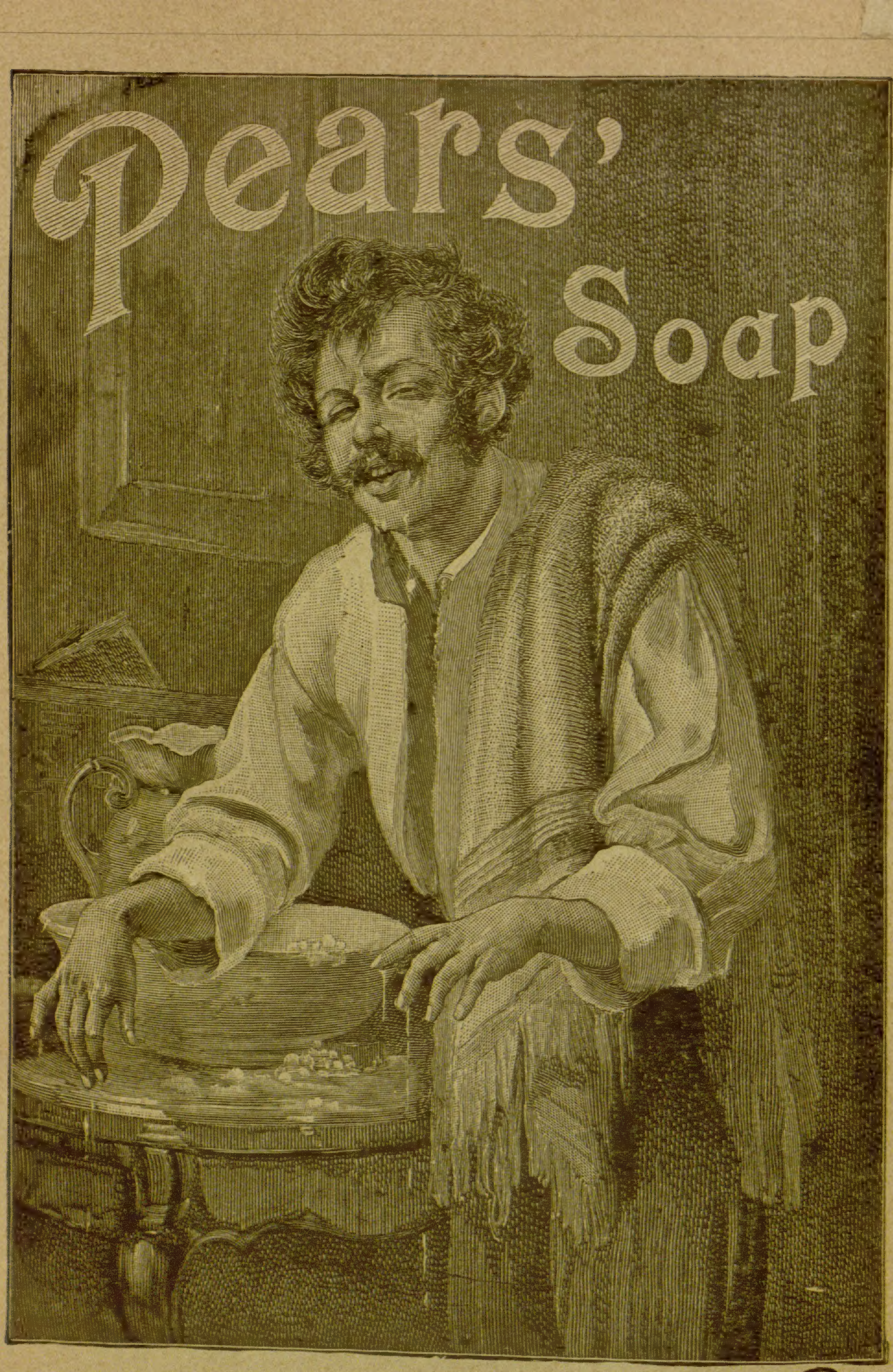

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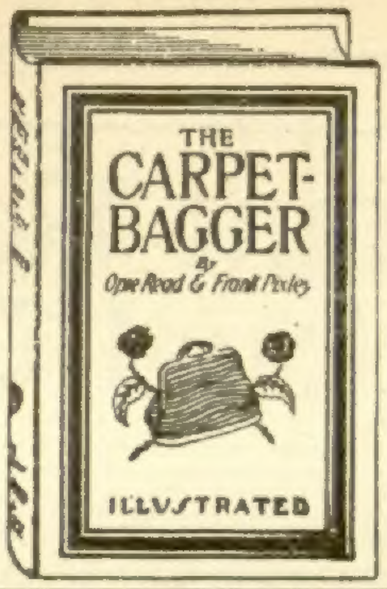

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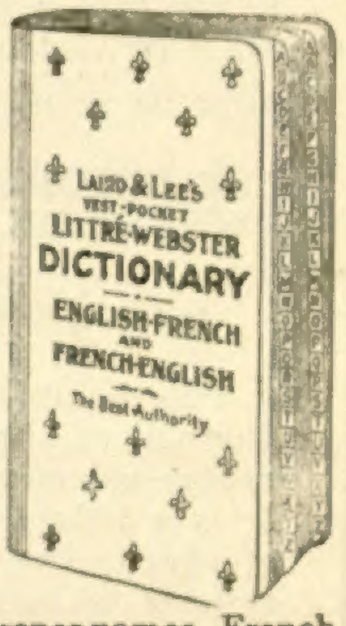

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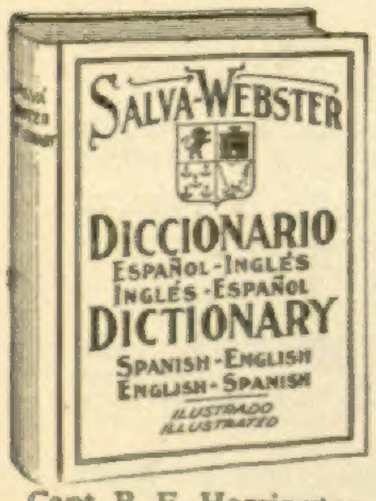

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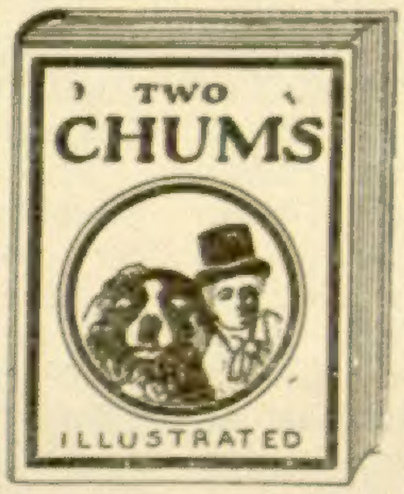

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VOLUME XXIX NUMBER 1

BOTANICAL GAZETTE

JANUARY 1900

THE MECHANISM OF ROOT CURVATURE.[1]

JAMES B. POLLOCK.

(WITH ONE FIGURE)

Introduction.

THE question as to the mechanism by means of which growing plant organs respond to external stimuli has engaged the attention of writers on the phenomena of plant life during the last hundred and fifty years. Some of the earlier writers supposed that plants turned toward the sunlight because the heat of the sun contracted the plant fibers on the side toward the light (1, 26). Du Hamel (15) assigned light as the cause of movement of leaves. He knew that stems grew upward in the dark and hence were not influenced in the direction of their growth by light alone, as had been supposed previously.

In 1806 Knight (31) published his classical experiments with seeds germinated on rapidly revolving wheels, and he found that the roots grew outward, and the stems inward toward the center of revolution. Knight drew the conclusion that gravitation is the force that causes roots of seedlings to grow down and stems

[1] The experiments reported in this paper were carried out at the University of Michigan in connection with work for the degree of Doctor of Science, under the direction of Professor V. M. Spalding. I wish to express my hearty thanks to both Professor Spalding and Professor F. C. Newcombe for many helpful suggestions and for the facilities of the botanical laboratory which were placed so unreservedly at my disposal.

to grow upward. This conclusion holds good to the present time, but Knight's explanation of how gravitation could affect roots so differently from stems is of historical interest only. He considered the root curvature as a purely passive bending due to great flexibility in the curving zone.

After Knight we need take no special notice of the explanations given of curvature in growing plant organs until the time of Hofmeister and Frank, though several authors (**4**, **16**, **40**, **70**) wrote upon the subject in the interval. The two men named engaged in a controversy as to whether the curve which takes place in roots that are placed in a horizontal position is purely passive as claimed by Hofmeister (**27**, **28**), or is an active curvature as asserted by Frank (**21**, **22**). The latter proved his point by showing experimentally that the curving root can be made to lift a weight. Frank also introduced the term *geotropism* to designate the response of plant organs to the action of gravitation.

Sachs, in his earlier work (**61**), explained the curvature of plant organs by supposing a difference in the rate of growth on the opposite sides of the curving organ. Later, influenced by the work of de Vries (**71–75**), he regarded the difference in growth of the two sides as conditioned by greater turgor on the convex side. De Vries's conclusions rested principally on the fact that plant organs in the early stages of curvature are completely straightened on plasmolysis, and he supposed the cells of the convex side must have been more highly stretched by osmotic pressure. The osmotic substances that were especially effective were said to be organic acids and their salts (**75**).

Sachs has added much to our knowledge of curvatures produced in plant organs by external stimuli. In his investigation of roots (**62**) he found that the cortex of roots grows faster than the axial strand, that split roots curve with the cut face concave, and that any part of the cortex derives its nutriment from that part of the axial strand lying in the same transverse zone. He found by external measurement, as well as by microscopical

measurement of cells, that in geotropically curved roots the convex side grows only a little faster than the normal root, while the strong curve is produced by the much reduced growth of the under side (**62**, p. 463). In another paper (**63**) he used stems of several dicotyledonous plants of different families, and, after separating different tissues of stems curved geotropically, he found that the concave cortex grows less and the convex cortex more than the corresponding parts in normal stems. Also the pith grows faster than cortex, and the relation of pith to cortex is such that in curved stems the tension is increased on the concave side and diminished on the convex side.

An interesting paper by Ciesielski (**5**) furnishes some valuable experiments in connection with root curvature, though his explanation of the curve is of no value. He was the first to assert that the removal of the root tip prevented the root from curving as usual when it was placed in a horizontal position. He cut off the cortex of roots on one side down to the axial strand, and when this side was turned downward with the root laid in a horizontal position the curve formed more rapidly and its radius was smaller than in the normal root under the same conditions. If such a root is laid with the cut face upward, in the majority of cases it curves downward likewise, though more slowly. Sometimes it curves upward at first and only afterward does it curve downward (**5**, p. 19). The significance of these experiments will be discussed later.

Kraus (**35**) investigated juice pressed out from the separated convex and concave halves of curving stems, and found, contrary to the theory of de Vries, that osmotic substances diminished both relatively and absolutely on the convex side during the progress of the curve. Hence the curve cannot be produced by an increase of such substances on that side.

Charles Darwin (**9**, **10**) gave a new impetus to investigation of curvatures produced by stimuli. His conclusion that the root tip performs a function similar to that of the brain in lower animals (**10**, p. 573) called out a great number of articles both for and against it, and the controversy only ended in 1894 when

Pfeffer (57) proved that Darwin was right, and that the root tip alone is sensitive to external stimuli, and the stimulus is transmitted to the part of the root in which the curve takes place, a distance which may be as much as ten millimeters. Darwin was also the first to show that injury to one side of the root tip may act as a stimulus, causing the root to curve away from the side injured. He regarded curvatures in growing organs as modifications of circumnutation, and thought the immediate cause was a difference in turgescence of the cells on opposite sides of a curving organ. In the work called out by Darwin's *Power of movement in plants* a number of new theories were evolved as to the mechanism of root curvature, and at first the theories had a very close relation to the question of the function of the root tip. Detlefsen opposed Darwin's view (13), but his purely mechanical explanation of the mechanism of curvature has been shown by Spalding (69, p. 442) to be untenable. Spalding adopts the term *traumatropism*, proposed by Pfeffer (56, p. 374) to designate a response of plant organs to the stimulus of injury or wounding, and this term has now been generally accepted.

Wiesner was probably Darwin's most vigorous opponent, and in several papers of considerable length (76–78) he discusses growth-curvatures in both stems and roots. He presents an explanation of these curvatures which, in a somewhat modified form, has been adopted by some of the most recent writers on the subject. He accounts for the traumatropic curvature of roots, which he calls the Darwinian curve, by an increased ductility of the cell membranes on the injured side. The turgor in these cells then stretches them more rapidly than those of the opposite side, with the result that a curve is produced whose convexity is on the injured side (78, pp. 268–9). The membranes of the convex side are not only more ductile, but also less elastic than those of the concave side. This condition is also favorable to the formation of a curve. The experimental evidence offered by Wiesner in support of his explanation of the curve was the fact that roots injured by decapitation grew faster than normal ones if they were grown in water, and even in those

grown in a moist chamber the partial growth in the zone of the traumatropic curve was greater than in the corresponding zone of normal roots, though the total growth of those in the moist chamber was less in decapitated than in uninjured ones.

In looking for an explanation of growth-curvatures which would apply to both unicellular and multicellular organs, Wortmann thought he had discovered the cause in the aggregation of the protoplasm on the side of the cell that becomes concave in the case of unicellular plants and a similar aggregation in the cells of multicellular plants on the side that becomes concave. This accumulation of protoplasm on the concave side had been noticed by Ciesielski (5) and Sachs, who wrote (65, p. 221) that it was not the cause but the result of greater growth on the side becoming convex. Wortmann thought (80) the protoplasm accumulated in the cells of one side produced a thickening of the cell membranes on that side. This thickening retarded growth in the longitudinal direction, and as the growth on the opposite side was not retarded, the organ curved, the side with the thickened membranes becoming concave.

Elfving (19) and Noll (48) have shown that the difference in the thickness of the membranes appears only after the curve is formed; hence it cannot be the cause of the curve as Wortmann supposed. Also Noll's measurement of the membranes in curved grass nodes (48) shows that the membranes on the concave side are not at all thickened, or only slightly more than the normal, but those on the convex side are much thinner than normal. Noll found in unicellular plants, walls unequally thickened on opposite sides of the organ which did not curve as it must have done had Wortmann been correct.

In partial agreement with Wiesner, Noll believes the curve is produced by a change in the quality of the membranes, those on the side which is later convex becoming more extensible. He seeks to prove this point by his bending experiments. Stems that were just beginning to curve were subjected to a pull at right angles to their long axes in the plane of the curve just beginning. This pull was exerted by a given weight for a

definite time, alternately toward the convex and concave sides. They always bent farther toward the concave side, and the conclusion was drawn that the membranes were more extensible on the convex side.

Noll sometimes found a shortening of the concave side of curving stems of Hippuris of 6–10 per cent. He quotes some figures from Sachs which show a shortening of 10–25 per cent. in nodes of maize (**48**, p. 528). He does not believe in the migration of protoplasm required by Wortmann's theory, nor did the latter offer sufficient proof of it. In plasmolyzing experiments Noll discovered at the beginning of plasmolysis a slight increase of the curve, followed only later by the straightening which de Vries had found. This increase of the curve on plasmolyzing does not take place after the curve is complete. Kohl confirmed these observations (**33**, p. 70). In a later paper (**50**, p. 84) Noll admits that his theory of the curvature does not fully explain this plus curve.

Both Wortmann and Noll seemed to start out with the hope of showing that the factors which produce the curvature operate on only one side of the curving organ, Wortmann finding them on the concave, Noll on the convex side. Both men, however, were compelled either by their own discoveries or by their critics to admit at least secondary changes on the other side.

In 1894 another theory of the mechanism of growth-curvatures was presented by Kohl (**33**). It may be called the *contraction theory*, and is supposed to account for the shortening of the concave side of curving organs, which had been reported previously by a number of observers. As a starting point, Kohl accepts Kraus's results that during the curvature osmotic substances increase on the concave side, and those of Noll in which plasmolysis shows a slight relative increase of turgor on the concave side, and confirms these results by plasmolyzing experiments in which he found constantly, in organs that were in the early stage of the curve, the protoplasm contracted from the walls of the cells on the convex side sooner than in those on the concave. He also found by microscopic examination that there

was a larger amount of copper-reducing substance in the cells of the concave side. Unable to accept either Wortmann's or Noll's views as to the cause of the curvature, Kohl elaborated the theory that the curvature is caused by an active contraction on the concave side, with a corresponding passive stretching on the convex side. The possibility of this contraction depends upon the fact, which can be mathematically demonstrated, that an oblong cell may increase in volume, and at the same time shorten its long diameter. Of course, the transverse diameter must increase, and the cell become more nearly spherical. The force that produces this shortening is the increased turgor of the cell, which, beyond a certain point, makes the cell shorter and broader, or, as Kohl expresses it, barrel shaped. It is at once seen that a condition necessary to the contraction of an organ in this manner is that the cells must lie with their long diameter parallel to the long axis of the organ. This condition Kohl himself seems to have overlooked, and it will help us to determine whether his theory is applicable to given cases of curvature.

In discussing the theoretical possibility of producing a contraction by increased turgor Kohl attempts to show that the conditions are favorable to it in stems where there are large intercellular spaces. Here we have what he calls alternately single and double membranes, the latter where two cells are in direct contact, the former where the cells border on intercellular spaces. To make this more clear, he compares this condition to an India rubber cell (**33**, p. 8) on the outside of which thicker strips have been fastened longitudinally. Now, if the India rubber cell is filled with water under pressure, it will stretch more in the transverse than in the longitudinal direction, because of the thicker strips in the latter direction. Here again Kohl overlooked a condition which must exist in organs with intercellular spaces, namely, that where the membrane is double the stretching force is doubled also, for a cell on each side of the membrane is stretching it in a longitudinal direction. Kohl probably got his idea of the contraction theory from some experiments of de Vries (**74**) in which he found that many roots,

especially fleshy ones which have a very large proportion of parenchyma tissue, contract by the absorption of water. Kohl agrees with Noll that at the beginning of the curvature there is no measurable difference in the thickness of the cell walls on the two sides, and that as the curve progresses the difference comes rather by thinning of the convex membranes than by a thickening of the concave membranes. Hence Wortmann's view cannot be correct. This view does not provide for a contraction of the concave side, a fact observed by former experimenters and confirmed by Kohl. He finds in Pisum that the cells of the concave side may shorten 19.4 per cent. of their normal length. Noll's theory as first enunciated provides for the shortening of the concave side only by a passive compression, though, as modified later, it allows a greater elasticity of the walls on that side.

In further support of his theory Kohl cites the fact that grass nodes, in curving, often break on the convex side with transverse clefts. This could not take place if the curve was produced by a greater extensibility on that side. This counts against Noll's theory, but is in perfect harmony with Kohl's theory which makes the lengthening of the convex side wholly a passive stretching. He shows by measurements in both stems and roots that the cells of the concave side become shorter and broader, and that those of the convex side become longer and narrower than normal.

Kohl thinks his theory accounts for the plus curve observed by Noll, though I cannot see the force of his reasoning. If increased turgor contracts the cells, decreased turgor ought to expand them. Noll showed (**50**, pp. 49–50) that this is not the case.

In a series of experiments Kohl cut transverse notches 2^{mm} apart in stems to the depth of the vascular bundles, and laid them in a horizontal position, some with the notched side uppermost, others with the notched side downward. The latter always curved more rapidly than the former, but Noll has shown that the difference was due to the traumatropic effect of the cutting. It is an interesting and perhaps a significant fact that when these organs curved water was forced out of the notches.

Some experiments on tissue tensions showed that when curved stems of Pisum were split into two equal parts both parts curved outward, that is, the concave side curved more and the convex side straightened. If the stem is split in parallel planes into three parts the concave cortex shortens and the convex cortex and pith remain about the same length. Kohl implies, though he does not directly say, that the tissue tensions indicated by the result obtained were due to the stimulus. In a footnote to his preface Kohl says he regards the stimulation curvatures as merely phenomena of tissue tension. Yet in his book (**33**) he devotes less than three pages to tissue tensions, and in his discussion he is only half right because he ignores the tissue tensions existing previous to the application of the stimulus and independent of it.

Pfeffer (**56**) reports some very searching experiments on stimulated grass nodes, and incidentally gives his views on the mechanism of curvature. The anatomy of grass nodes is very different from that of curving roots and most stems. The curving takes place only in the cushion of the leaf sheath at the node. The middle tissue of the cushion consists of a hollow cylinder of vascular bundles accompanied by a very large amount of collenchyma. This cylinder is bounded both internally and externally by thin-walled parenchyma. The tissue tensions are such that the parenchyma, freed from the bundles, lengthens 30–40 per cent., while the bundles contract less than 1 per cent. In the process of curving, when the grass stems are placed in a horizontal position, the growing collenchyma on the lower side frees the parenchyma on that side from its positive tension, and may even put it under a negative tension to such a degree that it is frequently broken in transverse clefts to the depth of the bundle. Thus the passive stretching of the convex side which Kohl supposed was produced by the contraction of the concave side, proves to be due to the reversed tensions between two tissues, both of which are in the convex side (**56**, p. 407). This applies to grass nodes only. Pfeffer's results prove conclusively that the contraction theory cannot possibly account for the curve in grass nodes, and Wortmann's theory is even less adequate.

As for the increased extensibility of the membranes on the convex side by which Noll accounts for stimulation-curvatures, it undoubtedly exists, but in the collenchyma, and not in the parenchyma. The change in the quality of the membrane is inferred by Noll both from a difference in the optical properties of the membranes, and from their decreased thickness and greater superficial area. However it is almost beyond doubt that in grass nodes this change in the quality of the membranes is a phenomenon of growth and is not a simple process of stretching, either plastically or elastically (**56,** pp. 405, 416).

In 1897 J. Loeb published a paper (**36**) in which he accounted for geotropic and heliotropic curvatures by a contraction of the concave side, not in the sense of Kohl's contraction, but in the sense in which the term is used in animal physiology. The contraction in plants is exactly the same as the contraction of muscles. Loeb thinks his theory is of universal application. It not only explains all the stimulation-curvatures of plants both unicellular and multicellular, but also those of animals (marine worms and hydroid polyps) and even puts phototactic and chemotactic movements of motile organisms on the same basis as heliotropic and geotropic curvatures. Loeb's plea for a simple explanation which will apply to all cases of movements and curves caused by stimuli has been anticipated and answered by Pfeffer. He says (**56,** p. 413): "The demand which is always recurring in relation to movements of curvature that the mechanics of the process be everywhere identical is only to be understood from the natural inclination to simplifying schemes, or from a narrow-minded view of living nature." Nature makes use of many means to accomplish similar ends. In its application to particular cases Loeb's theory is as inadequate to account for the curvature of grass stems as those of Wortmann and Kohl, and for the same reason, namely, it could not develop sufficient energy to accomplish the result, as Pfeffer's experiments prove (**56**). In the case of movements such as those performed by the pulvini of Mimosa and by sensitive stamens, water is given out into the intercellular spaces when the contraction takes place, and the shortened side

of the organ is not rigid but flaccid, while a contracting muscle takes up water (**36**, pp. 446, 447), and is more rigid than in the unstimulated condition. Loeb's theoretical explanation as to how gravitation causes a curvature presupposes that gravitation acts directly on the cells concerned in the curve (**36,** p. 448). This is not the case, however, in roots where the tip only is sensitive to the stimulus, and the changes in the cells where the curve is produced are brought about by an influence transmitted from the tip. The objections of Elfving and Noll to Wortmann's theory as applied to unicellular plants seem to me to be equally valid against the theory of Loeb for these plants.

An article on root curvature was published by D. T. MacDougal in the BOTANICAL GAZETTE for May 1897. Among other conclusions he has the following: "The curvature of roots is due to the excessive active elongation of the internal layers of the cortex, of the side becoming convex, made feasible by the increased stretching capacity of the longitudinal membranes. The extension of the membranes is accompanied or preceded by changes in the quality of the membranes as indicated by their reaction to staining fluids." MacDougal believes, then, that the convex side is alone active in producing the curvature, and he supports his view by measurements of cells on both the concave and convex side of curved roots, which are compared with measurements of cells in straight roots. The figures given show that, in the roots of *Zea Mais* curved geotropically 105°, the cells of the convex side are 3.2 times as long as those in the normal root, while the cells of the concave side are 2.1 times as long as the normal ones. Not only does the convex side grow much faster than the normal root, but the concave side also is much accelerated in growth. These results contradict the observations of several writers that the concave side often actually shortens, and indicate a rate of growth in stimulated roots which has not been observed by any other writer. I can only conclude that the cells measured in the normal root did not correspond to those measured in the curved root. The paper is obscure on the point as to how the author knew what cells to measure.

Apparently he took cells at equal distances from the tip in the normal and in the curved roots; but cells so situated would be comparable only if the two roots elongated at the same rate after the stimulation of the one, and this rate is just the point to be proved. To assume it, therefore, is to beg the question. MacDougal's results give further evidence that his "normal" roots were not normal. In his tables IX and X he gives results with roots bent mechanically, one after being geotropically excited one hour, the other without excitation. This latter one (table IX) must have been normal up to the time of bending, and as the author says the cells of the convex side have enlarged and those of the concave side diminished, the latter cells ought to be shorter than normal, but the figures given show the cells of the concave side in the root bent mechanically to be five times as long as the cells in his "normal" root. In the roots mechanically bent the curve of shortest radius coincides with that in roots geotropically excited; hence the latter are comparable to the former, taking into consideration the time element. If there is as much elongation in the region of greatest curvature of geotropically curved roots as MacDougal supposes, those which are geotropically excited and then bent mechanically ought to have longer cells than those bent without excitation, as both were bent 90°; but the figures show that cells on the concave side of roots stimulated before bending are little more than half as long as those bent without stimulation. Also the cells in the convex side of the former are only three fourths as long as those in the corresponding part of the latter. Looking at all the figures given by MacDougal, it is found that in all the roots curved geotropically the cells on the concave side are shorter than those on the same side of roots bent mechanically without stimulation; this is true even for the curves one hundred hours old, though here the growing tip has advanced 3^{cm} beyond the curve of greatest radius. Even the cells of the convex side of roots curved geotropically are shorter than those on the corresponding side of the roots bent mechanically, except in those curves which were seventy and one hundred hours old. So far from admitting

the correctness of MacDougal's conclusion, I am forced by a careful examination of his results to the view that roots geotropically stimulated shorten their cells on the concave side. This is shown even without taking his mechanically bent roots as the basis of comparison. Roots curved geotropically three hours through 60° have convex cells 43. 3° of the scale in length, concave cells 29.9°. Roots curved geotropically twenty hours through 105° have convex cells 48.05°, concave 24.7° of scale in length. Obviously, as the curve progresses, the cells of the concave side shorten 5.2° of the scale, the convex cells lengthen 4.7°. I am unable to explain the difference in the length of cells in the "normal" roots and those bent mechanically, as reported by MacDougal. So far as the paper makes it clear, they were supposed to be measured in corresponding regions. If the difference is due to individual variation it still vitiates MacDougal's conclusions. If it is due to the fact that the cells measured were not in corresponding regions, then the measurements in "normal" roots do not correspond to those in roots curved geotropically, for the author states distinctly (**39,** p. 346) that "The region of curvature artificially produced coincided with that of geotropically excited roots."

HISTORICAL SUMMARY.

In summing up the historical part of the question under consideration it is easily seen that no theory of the mechanism of the curvature yet advanced is satisfactory for all cases, and that the very different mechanical relations of tissues in different organs capable of curving make it extremely improbable that a single simple explanation will apply to all growth-curvatures. The causes of curvature as conceived in the different theories may be classified somewhat artificially as follows:

1. Difference in rate of growth on opposite sides of the organ. Sachs, Pfeffer (?).
2. Activity of protoplasm.
   a. By increased formation of osmotic substances on the concave side, accompanied by contraction. Kohl, Loeb.

b. By increased formation of osmotic substances on the convex side, accompanied by extension. De Vries.

3. Difference in the quality of cell membranes.
   a. Concave membranes thicker, more resistant. Wortmann.
   b. Convex membranes thinner, more ductile. Wiesner, Noll, MacDougal.

To be sure, all the theories must go back ultimately to the activity of protoplasm; but there is a question whether any factors are concerned in the curvature which are not concerned in ordinary growth, and whether the activity of the protoplasm is manifested in a change in its own condition, a change in the cell contents, or a change in the condition of the cell membrane. The curvature of grass nodes can be explained only by an increased growth of tissue on the convex side. Some contraction on the concave side is not excluded, but such contraction could not possibly develop energy enough to curve the organ. Plastic stretching on the convex side is also inadequate in grass nodes. Indeed, the changes in quality of the membranes on the convex side, which Noll has described, are similar to those which Strasburger has shown take place in cells of Cladophora when a new branch forms. Hence Noll's plastic stretching may be only a phenomenon of growth, and not a condition peculiar to curving organs. Increased growth on the convex side, however, will not explain the shortening of the concave side which has been reported by several observers. De Vries's view of increased turgor on the convex side is not tenable.

Original experiments.

MATERIAL AND METHODS.

In the following experiments a study was made of the traumatropic curvature of roots, and the materials used were the roots of *Vicia faba*, the broad or Windsor bean. Some of the experiments involved a separation of different tissues, and this species was chosen because of the large size of the roots, which were, therefore, easily manipulated, and in which the liability to

error was reduced to a minimum. With smaller roots it would have been impossible to separate the different tissues from each other with a sufficient degree of accuracy to make the results reliable. The seeds were germinated in moist sawdust, and when the roots had attained a length of from 1–5^{cm} the seedlings were removed from the sawdust, and placed with the roots projecting into water through holes in a thin board, the holes being of such a size that the upper part of the root fitted snugly, and the root was held in a vertical position pointing downward. The temperature of the water was regulated only by the temperature of the laboratory where the experiments were carried on, and was generally from 15°–20°C. No attempt was made to keep the temperature constant, and during the nights of the colder part of the winter it probably fell as low as 10°C. or lower; but as nearly all the observations used were made the same day the experiments were started, the fall of the temperature at night can have no effect on the results. The experiments were made with the roots in water rather than in moist air or sawdust, because the stage of the curvature could be seen in water without removing them and perhaps subjecting them to other stimuli; and it was found by trial that the results were much more uniform in water than in moist air.

At the time of removing from the sawdust or after they had been in water for some time, the roots were branded on one side of the tip by means of a hot piece of metal. A warm stage was heated by means of an alcohol lamp, and the roots, held at an angle of 45° or less from the horizontal, were placed with their tips in contact with the hot stage for an instant. The roots were then put into water as described before. In from one to four hours after branding they begin to curve away from the side that was branded, and when the curve had progressed sufficiently they were ready for further observations or operations. Control roots were nearly always used, and in selecting them they were generally paired off with the branded ones, so that the two sets should be as nearly alike as possible in point of size and stage of development. Roots that at first were inclined to curve

spontaneously were rejected. Further details in the treatment of the roots will be given in connection with the different experiments.

It will be necessary to understand the general anatomy of the root in the zone of growth. At the extreme tip of the root is a very well developed root cap which extends back as a sheath surrounding the whole root for 5^{mm} or more. Where the cap joins the tip of the root proper is the zone of initial cells or primary meristem. From this meristem are derived by cell division all the cells of both the cap and root proper. All the cells of the initial zone are completely filled with dense granular protoplasm. A very short distance above the initial zone, 1^{mm} or more, may be distinguished a central or axial cylinder composing, approximately, one third of the diameter of the root; and this central strand is surrounded by a cylinder of cortical parenchyma, characterized by numerous large intercellular spaces. These spaces are more conspicuous in the longitudinal than in the transverse direction, and may be followed very near to the initial zone. In sections of living roots these spaces are shown by the presence of air. Outside of the cortical parenchyma is the dermatogen layer, one or more cells thick. The cells of the dermatogen layer are more densely filled with protoplasm than the cortical layer, whose cells have a comparatively small amount of protoplasm, and a very large central vacuole. The cortical cells often have a large amount of starch in them. The outer layers of the axial cylinder are also densely filled with protoplasm and furnish the path along which the reserve food is brought from the cotyledons to the growing cells, as has been determined by experiment.

The cells of the initial zone are nearly isodiametric. The portions of the cortex nearest the initial zone often have the radial diameter of cells longer than the diameter parallel to the root axis.

Finally, all the cells come to have their longer diameter parallel to the long axis of the root. The cells of the axial cylinder elongate longitudinally much earlier than the cells of the cortex.

PATH OF TRANSMISSION OF STIMULUS.

As has already been stated, in these experiments it is regarded as settled that only the tip of the root is capable of receiving the stimulus, and that an impulse is transmitted from the tip to the zone of curvature which in the most typical cases has a region of maximum curvature from 3–5^{mm} from the tip. The whole zone of curvature is somewhat longer but seldom extends more than 8^{mm} from the tip at first. Afterward, by growth in length of the root, the curve may come to lie farther from the tip. Under favorable conditions the tip of the root may describe an arc of 90° in from three to four hours from the time of the branding; and in these cases, where the curve is rapid, it is found by careful measurement that the zone of maximum growth does not coincide with the zone of maximum curvature, but the latter lies nearer the tip than the former. Later, as the zone of maximum growth advances the two may coincide. These results confirm those of Weisner (78). The method used for ascertaining the path of transmission of the stimulus was suggested by Kohl's notch experiments on stems. The objection urged against his experiments, that the cutting itself acts as a stimulus, does not hold with roots, for as the tip alone is sensitive, cuts made back of the sensitive part do not appreciably stimulate it.

The method consisted in cutting off certain parts of the root before branding, and ascertaining whether the stimulus was transmitted in the part that was left, past the cut, or, to put it in another way, whether the root curved both above and below the cut.

In one set of experiments the root was cut with a sharp, thin bladed razor, in a plane exactly at right angles to the long axis, generally at a distance of from 2–3^{mm} from the tip, though sometimes from 3–4^{mm} from the tip. It was very noticeable that the nearer to the tip the cut was made the larger the number of responses to the stimulus in which the curve was on both sides of the cut or gash. In many of those in which the curve

did not extend above the gash there was a typical curve between the gash and the tip. The gashes were made deep enough to cut off the axial cylinder more or less completely, though as this could not be seen at the time of cutting, in many of the roots a small part of the axial strand must have been intact.

TABLE I.

ROOTS GASHED THROUGH AXIAL CYLINDER.

Date	Branded on opposite sides			Control, gashed but not branded	
	Distance of gash from tip	Roots used	Roots curved	Roots used	Roots curved
1896					
Nov. 7	2.5–3 mm	3	3		
10	2	4	2		
11	2	6	3		
12		8	6	8	1
14		4	0?		
17		17	7		
23		5	2		
26	3–4	8	3		
30		14	4		
Dec. 1		8	6		
2	3–4	7	3		
3	3–4	8	3		
4	3–4	8	1		
1897					
Mar. 18	2–3	8	6		
		108	49		

Table I shows the different lots in a series of experiments in which the gash was made through the axial cylinder and the roots were branded on the opposite side of the tip. In the second column the blank spaces mean that no record was made of the distance from the tip at which the gashes were made. In the fourth column the numbers show how many of the roots curved away from the brand both above and below the gash. Many more of them showed a traumatropic curve between the gash and the tip, and this was especially true of those in which the gash was made 3–4 mm from the tip. It may be objected that there are not enough control roots, but many of these lots were

observed at the same time as other sets, which will be shown in other tables, and these acted as control experiments for each other. For instance, those in which the brand was on the opposite side from the gash served as control for those in which the gash and brand were both on the same side.

A total of one hundred and eight roots were gashed in the manner indicated in the table, and branded on the opposite side of the tip. Whatever traumatropic effect the gash would have on the root would, in this case, work against that of the brand. Of these roots forty-nine, equal to 45.3 per cent. of the whole number, curved away from the brand both above and below the gash. These roots were tested in lots, the number varying from three to seventeen in each lot. The observations must be made within five or six hours after branding, for after that time some that have shown the curve more or less plainly begin to straighten, and after twenty-four hours a much smaller number will show the curve above the gash.

TABLE II.

ROOTS GASHED THROUGH AXIAL CYLINDER.

Date	Branded on same side			Control, gashed, not branded	
	Distance of gash from tip	Roots used	Roots curved	Roots used	Roots curved
1896					
Nov. 10	2mm	5	1		
11		7	4	5	1
12		8	4		
13		5	0		
14		6	1		
16		12	9		
23		5	4		
25		11	5		
1897					
March 19	2–3mm	9	4	9[a]	8
20	2–3mm	8	6	8	1
		76	38		

This table shows that 50 per cent. of the roots curved both above and below the gash, when the brand and gash were on the

[a] These nine were branded, but not gashed.

same side, about 5 per cent. more than when they were on opposite sides. It is possible that the gash in some cases was near enough to the receptive part to give a slight stimulus, whose effect was added to that of the brand. Of the two lots marked "control" which were gashed, but not branded, one of the five showed a distinct but not great curve away from cut side, and in the lot of eight the one that curved away from the cut had the cut only 2^{mm} from tip.

TABLE III.

ROOTS GASHED IN CORTEX ONLY.

Date	Branded on gashed side			Control, gashed, not branded	
	Distance of gash from tip	Roots used	Roots curved	Roots used	Roots curved
Nov. 10		5	4	4	1
11	2^{mm}	7	1	5	0
7	$2.5-3^{mm}$	3	3	3	1
12		8	6	8	1?
28	$2-3^{mm}$	9	5		
		32	19	20	3

In these experiments, where a large part of the cortex and all the axial cylinder were left intact, 59.3 per cent. of the roots curved both above and below the gash. Taking from the three tables all the control roots that were gashed, but not branded, we have a total of forty-one roots, of which six showed a curve away from the cut. In a few of these cases it was somewhat doubtful whether the curve was really the effect of the wound or simply a spontaneous curve. But, considering them as due to the cut, we have 14.6 per cent. curving from the effect of the cut. This is a greater difference than is indicated by the two sets of experiments where effects of the cut and the effects of the brand worked with each other in one set and against each other in the other set.

TABLE IV.

ROOTS GASHED ALL AROUND IN CORTEX ONLY, AND BRANDED ON ONE SIDE OF THE TIP.

Date	Distance of gash from tip	Hours after branding	Roots used	Roots curved	Curved only below gash
1896					
Nov. 13		4	8	0	6
14		6	6	0	4
16		24	16	0	8
17		5	16	0	few
18	3–4 mm	7	6	1	5
20		7	9	0	7
23		6	12	2	8
25	2–3	6	10	7	2
26	3–4	5	9	4	3
28	4	4	10	1	8
28	2	24	9	3	3
30	2–3	5	8	4	1
Dec. 7	3–4	6	10	1	1
7	2	12	10	1	?
8	2	7	10	3	0
8	3–4	10	10	2	7
10	2–3	6	10	3	1
10	3–4	6	10	0	7
15	2–3	11	20	4	3
17	2–3	7	20	7	0
1897					
March 17	2–3	4	6	3	1
			225	46 20.4%	76 33.7%

In this table the third column indicates the number of hours after branding when the observations here recorded were made. These were not necessarily the only observations, as with nearly all lots several observations were made at intervals of two or three hours, then again after twenty-four hours. In making up the tables those results were taken which showed the largest number curved. The column headed "roots curved" shows the number that curved both above and below the gash. The last column shows the number that curved between the gash and the tip in addition to those in the preceding column.

It is seen that in these roots in which the cortex is cut off as completely as possible only 20.4 per cent. of the roots curve, though the axial cylinder was practically all present. Owing to

the impossibility of cutting exactly to the required depth, small parts of the cortex were probably left in many of the roots. Putting together the results of the last two columns, we see that more than 50 per cent. of the roots curved in some degree away from the brand. Hence the cutting did not inhibit the curvature as might be objected, but kept it below the cut in the large majority of cases.

TABLE V.

AXIAL CYLINDER OF ROOTS CUT OFF BY STABBING.

Date		Branded on same side as stab		Branded on side opposite to stab		Branded on side 90 from stab	
1896							
Nov.	16					16	2
	17					16	3
	18					7	5
	19			11	8		
	20	12	6	10	3		
	21			10	6		
	21	9	5	10	8		
	21			9	6		
	23			7	5	13	12
	24					9	7
	24	9	9			9	7
	25					9	5
	27			9	9	9	6
Dec.	7					10	7
	7					10	4
	9					10	7
	9					10	3
	15					20	10
	17					20	14
1897							
March	13					9	6
	15					14	11
	16					17	16
	•						
		30	14 46.6 %	66	45 68.1 %	208	125 60.0 %

Table V is instructive as evidence on the question of the transmission of the stimulus. All the roots had the axial cylinder cut off as completely as possible, in such a way as to leave as much of the cortex as possible. The cutting was done with a long slender pointed scalpel, so narrow that it could be pushed through the root, cutting off the axial cylinder, but leaving most

of the cortex intact on two opposite sides. Some of the cortex necessarily had to be cut in getting to the axis, especially on the side where the scalpel was pushed in. A small amount of cortex was also cut on the side opposite to this, for the scalpel had to be pushed through till its point could be felt on the farther side. Part of these roots were branded on the side from which the scalpel was pushed in, part of them on the side opposite, and part of them 90° from that side. A total of 304 roots were used, and of these 184 curved away from brand both above and below the stab in the root. That is, 60.5 per cent. showed the typical traumatropic curve more or less distinctly.

The lot of sixteen tested November 16 was not looked at after branding for twenty-four hours, or the result might have been different. I cannot explain satisfactorily the low result on November 17 and 20, unless the stab was made too far from the tip. In most of the lots the stab was made between 2 and 3^{mm} from the tip, and the roots were looked at several times within the first eight hours after branding as well as twenty-four hours after. The results were taken when they showed the greatest number curved. The necessity of control experiments in which the roots should be stabbed and not branded, was obviated by branding on different sides as related to the position of the stab. Thirty-six control roots were branded, but not stabbed, and twenty-nine of them curved away from the brand, 80.5 per cent. In roots branded under the most favorable conditions only about 5 per cent. fail to show the traumatropic curve.

In order to be certain that the stimulus was not transmitted in parts of the axial cylinder which might not have been cut off, many of them were afterward examined microscopically. In an especially favorable lot of seventeen roots, of which sixteen showed the traumatropic curve both above and below the stab, twelve of them had the axial cylinder completely cut off, and those that had the axial cylinder partially intact were among those that curved least and straightened soonest.

Six hours from the time of branding some of the roots that had curved somewhat were already beginning to straighten.

The stabbed ones did not curve so much as the control, and a larger percentage of them straightened within twenty-four hours. A possible source of error is seen here, since, if observations are not made within a few hours after branding, the root may have already curved and straightened. This may account for the negative results in some of the earlier lots.

If we leave out the first two lots of sixteen roots each in which the results are so low, we get exactly the same percentage of curved roots, 68.1 per cent., in both those that were branded on the side opposite to the stab and those that were branded on the side 90° from the stab. This is only 11.9 per cent. less than the control roots which were branded and not stabbed. This difference might easily be due to the inhibiting or paralyzing action of the injury.

Putting together the results of these experiments, it is seen that the transmission of the stimulus past the cut depends very largely on how much of the cortex is present. The lowest percentage of curved roots (20.4 per cent.) was found in those that had the axis complete, but much of the cortex cut off (table IV). The highest percentage of curved roots, 60 per cent. and 68.1 per cent., was found among those in which the axis was completely cut off, but the cortex mostly present (table V). The results in tables I, II, and III show a curving in proportion, roughly speaking, to the amount of cortex present. When the axis, as well as a large part of the cortex, was left intact 59.3 per cent. curved on both sides of the cut, only 1.2 per cent. less than when the axis was cut off completely.

We are therefore justified in drawing the following conclusions:

1. The stimulus can be, and is, transmitted in the cortex.

2. While it is not absolutely demonstrated that the impulse cannot be transmitted in the axial cylinder, it seems very probable that it is not transmitted there.

3. The impulse that affects the part of the root above the cut can be transmitted in the cortex of either the concave or the convex side.

4. The stimulus can also be transmitted transversely, or at least tangentially in the cortex. This follows from the fact that the curve was formed when only a small part of the cortex was left either on the concave or convex side. The stimulus, after passing the cut on one side, still influenced the cells on the opposite side to aid the curve.[3] This is a fact which every theory of curvature must take into consideration.

5. The experiments in table II disprove Wiesner's theory of the traumatropic curvature of roots. He says decapitation of the root tip accelerates growth in the region of the curve by making the walls more ductile. Injury to one side of the tip increases the ductility of the membranes on that side of the root; hence it grows faster than the other and the curve results (**78,** p. 268). If Wiesner's view were correct the gash on the same side of the root as the brand would prevent any curve above the gash; since neither the stimulus nor any tensile strain could be transmitted across the cut. As the root does curve above the gash Wiesner's view cannot be correct. The process is more complicated than he supposed.

6. These results seem to show that both sides are concerned in the formation of the curvature, certainly to the extent of conducting the stimulus, and if to that extent probably both sides are also concerned in the changes in the cells that produce the curve directly. This point will be discussed more fully later.

TISSUE TENSIONS.

It has long been known that the pith of dicotyledonous stems grows faster than the cortex, and that as a consequence there is considerable tension between these tissues. The pith is under positive, the cortex under negative tension, so that when the stem is split in the growing part the two halves bend outward, the cortical side becoming concave, the pith side convex. In the normal stem the tensions between the pith and the cortex of any

[3] Czapek (**7**) has recently shown, by the same method that I have used, that the stimulus can be transmitted in a transverse direction in roots. A *résumé* of my own experiments was first published in the Proceedings of the American Association for the Advancement of Science for 1897.

side tend to curve the stem toward that side. But this is balanced by an equal tendency on the opposite side to curve in the opposite direction, and the stem remains straight. The potential energy of this normal tension is available for producing a curve as soon as the equilibrium of tension is disturbed. This equilibrium may be disturbed either by an increase of tension on one side, in which case that side will become concave, or by a decrease of tension on one side, in which case that side will become convex, or both these changes may occur. Kohl (**33**, p. 87) thinks the first of these alternatives is the true one, because when a curved stem is split in halves the convex half straightens or curves in the direction opposite to that of the whole stem. Kohl does not make sufficient allowance for the tissue tensions which are present previous to stimulation. The convex half of the curved stem will curve more in the original direction when separated from the other half, only in the case in which the tension on the convex side is reversed from the normal, that is, where the cortex becomes longer than the pith. This probably seldom happens. Kohl's experiments taken with those of Sachs (**63**), in which curved stems were separated into three strips, concave cortex, pith, and convex cortex, show very conclusively that the stimulus influences the tension *on both sides of the curving stems*, and that the tension is decreased on the convex side, and increased on the concave side. Sachs' experiments also show that the deviation from the normal is greater on the concave side than on the convex side, that is, the increase of tension on the concave side is greater than the decrease on the convex side. These tension relations explain the results of Noll's bending experiments, from which he draws the conclusion that the membranes of the convex side are more extensible than those of the concave side, because the stems bend more easily toward the latter side. However, increased tension between the pith and cortex of the side becoming concave, even without the decreased tension on the opposite side, causes a greater resistance to bending toward the convex side than toward the concave. Hence Noll's conclusion does not at all follow from his

results. Without at present going into the question as to how stimuli cause the changes in tensions of normal stems, it seems very certain that changes of an opposite kind are produced on opposite sides of curving stems. Those writers, therefore, who attempt to explain stimulation-curvatures by a change on only one side of the curving organ are overworking a half truth.

On taking up the study of roots the question presents itself as to what the tissue tensions of roots are and how stimuli affect them. Hofmeister asserted that there were no tissue tensions in roots. More recently Pfeffer has written (**53,** p. 31): "In the zone of roots in which growth in length takes place, in spite of differentiation of tissue, only a slight longitudinal tension is shown." . . . "A certain negative tension is to be assumed for that part of the axial vascular cylinder which is still capable of growth, since a gradual curve results with the concavity toward this part, if a root split longitudinally is kept under proper conditions." Pfeffer refers to the experiments of Sachs (**62,** p. 435) for the truth of his statement. My own experiments lead me to believe that the tissue tensions of roots are more important than has been supposed, and that they play a considerable part in the formation of curvatures. That the tension between the axial cylinder and cortical parenchyma in roots can become considerable is shown by the fact that in *Vicia faba* roots growing rapidly in water the axial cylinder is frequently ruptured transversely by the more rapidly growing cortex. These breaks in the axial cylinder become visible only when the root is cut into longitudinal sections, and I have found as many as six breaks in the same root within a piece of the root 2–3^{cm} long. Besides the method used by Sachs to show tissue tensions of roots, namely, splitting them into longitudinal halves, I have also used the method he and others have applied to stems. If the cortex is carefully separated from the axial cylinder and the separated lamellae left attached to that part of the root above the zone of separation, the lamellae of the cortex project beyond the axial cylinder. If the tip of the root is cut off square before the separation, the difference in length after separation becomes visible

to the unaided eye, and usually may be measured with an ordinary millimeter scale. A root of *Vicia faba* whose total length was 1.5^{mm} had its cortex separated from the axial cylinder in the zone of growth, and immediately afterward was laid in water. After ten minutes the isolated strips of cortex were 9^{mm} long, and the axial cylinder was 8^{mm} in length, a difference of 12.5 per cent. computed on the length of the axial cylinder. To compare this difference with that found in stems we may take the figures given in Sachs's *Text-book*, English edition, pp. 798–9, where the greatest difference in length of pith and epidermis of stems of *Silphium perfoliatum* is 13.4 per cent. This would probably have been somewhat greater had the pith and epidemis been separated from each other. Nevertheless the comparison shows that the amount of difference in the length of isolated tissues of roots may approach that of stems. It does not follow that the tissue tensions in the growing zone of roots represent as much potential energy as those of stems. The resistance of the tissue under negative tension in roots is much less than that of the tissue under the same tension in stems, and for the reason that the vascular bundles are so incompletely developed in the growing zone of roots. This explains why the axial cylinder of roots is often broken by the negative tension to which it is subjected, and also why the halves of split roots do not always curve with the cut face concave immediately after splitting. This curve always follows sooner or later provided the halves continue to grow, except when the root is laid in a horizontal position with the cut face upward. Often in roots growing rapidly the curve follows at once after splitting.

The root on which the above measurements were made was afterward plasmolyzed in 10 per cent. KNO_3. The cortex shortened 1^{mm}, the axial cylinder, 0.5^{mm}. In some cases the axial cylinder shortens more than the cortex, a fact which the tables do not show. The fact that the axial cylinder is shorter than the cortex after plasmolysis proves that the difference in length is not due merely to turgor, but that there is normally a difference in the rate of growth of the two tissues.

The separation of the cortex from the axial cylinder was done by first cutting off the cortex with a sharp razor on two opposite sides, in to the axial cylinder, for a distance from the tip equal to the length of the growing zone. This left a lamella of the root consisting of the axial cylinder, with a narrow strip of cortex on two opposite sides. Then 1^{mm} of the tip was cut off exactly transversely. With a very fine-pointed, thin scalpel the strips of cortex were separated from each other, but all left attached to the upper part of the root. The separation can be made quite accurately with roots as large as those of *Vicia faba*. The operation left the strips of tissue free to curve or straighten, lengthen or shorten. The time required to perform the operation was two or three minutes, and the roots were dipped in water several times during the operation to prevent wilting. After the separation they were laid in water and were observed for changes during several minutes.

TABLE VI.

POSITIVE TENSION OF CORTEX IN STRAIGHT ROOTS AS SHOWN BY DIFFERENCE IN LENGTH ON FREEING FROM AXIAL CYLINDER.

	In water				In KNO_3 10%			
Date 1897	Roots used	Cortex longer than axis	Cortex shorter than axis	Cortex and axis equal	Roots used	Cortex longer than axis	Cortex shorter than axis	Cortex equal to axis
January ?	8	7		1				
March 29	10	5	1	4	9	6	2	1
March 30	10	5	2	3	7	6		1
April 20	16	15		1	15	13		2
	44	32	3	9	31	25	2	4
		72.7%	6.8%	20.5%		80.6%	6.5%	13%

In these experiments the roots were observed especially for the difference in length between the cortex and axial cylinder after the strips were separated from each other. Forty-four roots were observed in water, and thirty-one of these were plasmolyzed in 10 per cent. KNO_3. In almost three fourths of the roots the cortex was longer than the axial cylinder when they were placed

in water, and on complete plasmolysis a still larger proportion showed the cortex longer than the axial cylinder. This difference in length was often greater in the same root after plasmolysis than before. The observations were made with the unaided eye or with a lens of about ten diameters. Even though there was a small number of roots in which the cortex was under negative tension, it is clear from the table that in the large majority of cases the cortex is under positive tension and the axial cylinder under negative tension.

A series of experiments designed to ascertain the effect of stimulation on tissue tensions, as indicated by difference in length of separated tissues, is shown in table VII.

TABLE VII.

EFFECTS OF STIMULATION ON TENSION.

Date 1897	Roots used	x longer than v, v longer than a	$x=v$, both longer than a	x longer than a, v shorter than a	x longer than a, $v=a$	$x=a$, v shorter than a	x shorter than a, v shorter than x	
January 16 - -	1	1						In water
April 20 - -	22	6	2	5	8		1	
March 30 - - -	7		2	4	1			
	30	7	4	9	9		1	
		23.3%	13.3%	30%	30%		3.3%	
January ? - -	2						$x-v$ both$=a$	In 10% KNO_3
March 30 - -	6			1		1		
April 20 - - -	23	2	1	3				
	31	9	2	4	3	3	2	
		11	3	8	3	4	2	
		35.5%	9.6%	25.8%	9.6%	12.9%	6.4%	

In these experiments the roots were branded and as soon as they began to curve, or while the curve was in progress, they were sliced and split as before in such a way that the three strips of concave cortex, axis, and convex cortex lay in the plane

of the curve. In the table x stands for the strip of convex cortex, v for concave cortex, a for the axial cylinder. The first part of the table shows the relative length of x, v, and a in water, the second part in 10 per cent. KNO_3. Sometimes the cortex curved away from the axis, and had to be held in place in order to see their relative length. In doing this care was taken not to push the axis out of the position it naturally took. Most of the roots were somewhat curved, and if they were forcibly straightened, x was always longer than a, and v nearly always shorter than a. The time of splitting varied from 1.5–6 hours after branding.

From the table it is seen that in water 23.3 per cent. and in KNO_3 35.5 per cent. of the roots showed both strips of cortex longer than axis and the convex side longer than the concave. In 13.3 per cent. of those in water and 9.6 per cent. of those in KNO_3, x and v were equal but both longer than a. In water x was shorter than a in 3.3 per cent., in KNO_3 x was equal to a in 6.4 per cent. of the roots.

In water x was longer than v in 86.6 per cent. and longer than a in 96.7 per cent.; v was longer than a in 36.6 per cent., equal to a in 30 per cent., and shorter than a in 33.3 per cent. of the roots.

In KNO_3 x was longer than a in 80.5 per cent., and longer than v in 83.8 per cent.; v was longer than a in 45.1 per cent., equal to a in 16 per cent., and shorter than a in 38.7 per cent. of the roots.

All the measurements in this table are merely relative and not absolute. It is not shown from these experiments that the tension is increased on the convex side, but it is shown beyond a doubt that it is decreased on the concave side to such an extent that in about one third of the cases it was reduced to zero, and in another third was reversed, the cortex of this side becoming negative with respect to the axis. This shortening cannot be merely by compression, for there is not sufficient lengthening of the convex side above the normal to account for so much compression. Hence the stimulus causes a change in the cells of

the concave side that at least prevents them from lengthening in proportion to the axis and the convex cortex.

TABLE VIII.

ROOTS BRANDED AND SPLIT INTO HALVES AFTER CURVE HAS BEGUN.

Date 1897	Roots used	Hours after splitting	*z* and *y* curved in	*z* curved in, *y* out	*z* curved in, *y* straight	Both *z* and *y* straight
Jan. 27	3	4	1		2	
28	6	1.5	1	5		
29	4	1		1	3	
30	5	0.5		1	4	
Feb. 1	11	2.5	6	1	2	2
2	7	1.5	2	4	1	
3	3	1.5		1	2	
4	5	4	3		2	
5	5	3	1	4		
8	5	1.25		5		
9	6	5	1	4	1	
10	10	2		3	4	2
	69		15	29	21	4
			21.7%	42%	30.4%	5.8%

In the experiments shown in this table, the roots were branded and placed in water until the curving had begun. They were then split into two equal parts by means of a sharp thin scalpel, in such a manner that one half was the convex side and the other the concave side. The branding was done at such a point that when the roots were split completely one cotyledon remained attached to each half, so each half could get its supply of materials for growth. The halves were separated from each other completely, and the half roots were all placed in water in an upright position. By *curving in* is meant that the tip of the half root turned toward the cut face. *Curving out* means that the tip of the half root turned away from the cut face. The letter *z* stands for the convex half, the letter *y* for the concave half of the curve that was due to the branding. The two halves of the same root were kept so that they were compared with each other, and the numbers in the right hand column of the table stand for whole roots, the two halves of which behaved as

indicated at the top of the column. The discussion of this table will be taken up in connection with tables IX and X.

TABLE IX. CONTROL FOR TABLE VIII.

STRAIGHT UNINJURED ROOTS SPLIT INTO HALVES AT THE SAME TIME AS SOME OF THE BRANDED ONES.

Date 1897	Roots used	Hours after splitting	Both halves straight	Both curved in	Both curved out	One in, one out	One straight, one out	One straight, one in
Jan. 27	3	3.5	1		2			
28	4	1.5		2		2		
29	3	1		3				
29	4	2.5	1	2			1	
30	5	0.5		2				3
Feb. 1	5	2.5	1	2				2
2	4	1.5	3				1	
3	3	1.5	3					
4	3	4		3				
5	5	3		5				
8	4	1.25	1			3		
Apr. 13	8	6		8				
	51		10	27	2	5	2	5
			19.6%	52.9%	3.9%	9.8%	3.9%	9.8%

This table shows the results with roots which were straight and not branded, but which were split at the same time as branded roots shown in tables VIII and X. The lots that are directly comparable may be known by looking at the date and the column showing the hours after splitting at which the observations were made. Thus all the lots in table IX, except one on January 29 and one on February 4, may be compared with lots in table VIII.

It will be seen that 52.9 per cent. of the roots shown in table IX had both halves of each root curved in toward the cut face at the time the record was taken for the table. Sooner or later all the halves that grew at all, curved in this way. This latter fact the table does not show. The different series may be compared in several ways to show the effect of the branding; first, as to the number of roots that show a given curve at a given time; second, as to the extent of this curve; third, as to the

time at which the curve begins. The first and third of these are the only comparisons that can be made from the tables. The second will be shown by a diagram.

TABLE X.

ROOTS SPLIT INTO HALVES AND AFTERWARD BOTH HALVES BRANDED ON OUTER SIDE OF TIP.

Date 1897	Roots used	Hours after branding	Both halves curved in	One straight, one curved in	Both straight
Jan. 27	2	3.5	1	1	
29	4	2.5	4		
Feb. 3	3	1.5	1	1	1
4	5	4	5		
5	5	3	3	2	
Apr. 13	8	6	8		
	27		22	4	1
			81.4%	14.8%	3.8%

It may be objected that these tables are not comparable because the time element is not constant. This objection is met by the fact that if we take table IX for the control of both VIII and X we have the time element varying similarly in the different tables. With a few exceptions the lots of the same date were under exactly the same conditions including the time element. Leaving out the exceptions and taking only those lots that were under the same conditions in all particulars, we get a different numerical result, but the general showing of the tables is the same. The numerical change is this: 69.2 per cent. of the roots treated as in table IX correspond to 81.4 per cent. of those treated as in table X. These had both halves curved in toward the cut face. Also 42.4 per cent. of the roots in table IX correspond to 19.0 per cent. of those in table VIII. These also had both halves curved in.

Making due allowance for the variation of the time element a number of facts become apparent. In roots that have begun to curve when they are split, the half nearest to the brand, the

convex side, goes on with its curving as rapidly as, or more rapidly than, the whole root would have done. The opposite half, the one that would have become concave in the whole root, may also curve more than at the time of splitting, but this curving is not invariable. This half may remain stationary for some time, then begin to curve toward the cut face, and therefore toward the brand. This curving in, however, has been delayed by the branding and only 19 per cent. of these roots have both halves curved in at a time when 42.4 per cent. of the control roots have both halves curved in. In the time that 69.2 per cent. of the control roots show both halves curved in, 81.4 per cent. of those that were branded on outer side of both halves show the same condition. Obviously, then, branding increases the rapidity of the curving of the convex half of the root. The other half of the root usually does not continue the curving away from the brand, but it is considerably delayed in curving in toward the cut face, which nearly always takes place sooner or later in both control and branded roots. These facts, on first thought, seem to indicate that only the convex side is active in producing the curve of the whole root. That does not follow, however, when it is remembered what the tensions of the root are previous to stimulation. The concave half of the root when separated will curve outward only when the stimulus has reversed the tensions on that side and put the cortex under negative tension in relation to the axial cylinder. If the tension were originally at the maximum for roots it could be considerably decreased on the concave side, and yet that half of the root could curve toward the cut face when separated from the other half. The fact that the concave half of the root sometimes curves farther, after separation, in the direction of the curve of the whole root, shows undoubtedly that the tension is sometimes reversed. In the cases in which the separated concave half curves no farther outward, the delay in curving with the cut face concave indicates that the original tension on the concave side was decreased but not reversed by the stimulus. Further experiments will be offered on this point.

In comparing split roots, both halves of which have been branded on the outer side of the tip, with control roots that have likewise been split but not branded, a notable difference is seen after a few hours from the time of branding both in the localization and the amount of the curve. *Fig. 1* shows this difference, *a* being a half root that was not branded, and *b* one that was branded on the outer side of tip. These curves were projected directly on paper, and show about the average condition in a set of sixteen roots, all of which were split throughout the length, with a cotyledon attached to each half root. The half roots were paired with their original fellows, and eight roots had both halves branded on the outer side of the tip; eight were not branded. Six hours after splitting all the branded half roots except one are curved more than 90°, and the curve is localized in the region in which the traumatropic curvature takes place. Only five half roots out of sixteen not branded had curved as much as 90°, and the curve extended over a longer zone of the root. In these roots there was no difference in the time after splitting at which the curving began. This is only one set out of a number which showed the same general result. This result shows conclusively that the stimulus increases the tissue tension on the convex side of roots in the zone in which the traumatropic curvature is produced.

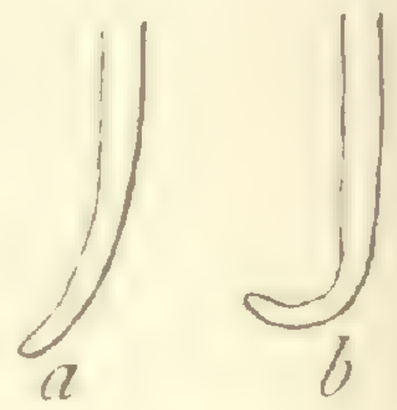

FIG. 1.

In the experiments shown in table XI roots were used that were already curved from branding, but in which the curve was still progressing, and in which, therefore, the conditions that bring about the curvature were still present. The roots were split at a time after branding which is indicated in the second column. The roots were sliced and split according to the method employed for table VII, and the three strips of convex cortex, axial cylinder, and concave cortex were observed with special attention to the curving of the parts after separation. The lettering is the same: *x* stands for the convex cortex, *c* for the concave cortex, and *a* for the axial cylinder. In a comparatively large number of cases both *x* and *c* pull away from *a*, *x* straightening

and *v* curving more strongly, but it was very noticeable that *v* pulled much farther away from *a* than *x* did, often forming a half-circle or more, and doing this with a sudden jerk as soon as it was free to do so. In other cases *x* lay up close to *a*, as before separation. These two cases are combined in column four, which shows the number, 55.8 per cent., in which *v* pulled farther away from *a* than *x* did. In this column *x* may either have pulled away from *a* or not.

TABLE XI.

MEDIAN SLICE OF CURVED ROOTS SPLIT INTO THREE STRIPS, CONVEX CORTEX, CONCAVE CORTEX, AND AXIAL CYLINDER.

Date. 1897	Hours after branding	Roots used.	*v* curves from *a* more than *x*	*v* and *x* curve more than at first	*x* curves from *a* more than *v*	*x* and *v* curve equally from *a*
Jan. 13	2	1	1			
14	2–4	6	4		1	1
15	3–4	3	1	1	1	
16	2–3	5	4			1
18	4	5	5			
19	2–4	6	3	3		
19	7	2	2			
20	2–3	2	2			
March 29	4–6	6	2	4		
30	4	7		7		
		43	24	15	2	2
			55.8%	34.8%	4.7%	4.7%

In the fifth column is shown the number of roots in which both *x* and *v*, after separation from *a*, increased their curve in the direction of that of the whole root; 34.8 per cent. of the total did this, though only four different lots showed it at all. Only a very small number showed *x* pulling away from *a* more than *v*, or *x* and *v* standing at equal distances from *a*. These experiments show that, aside from the difference in tension between cortex and axial cylinder the stimulus may also cause such a tension within the cortex of either side that it tends to curve away from the brand when completely free from other tissues. The next table will show that there is no such tendency in roots not wounded at one side of the tip.

It might be supposed that there was a contradiction between the results of table XI and those of former tables. Here we find the concave cortex showing a stronger tendency to curve than the convex cortex, but in the former tables we found that on splitting curving roots into two equal parts only the convex half continued the curvature away from the branded side, while the concave half usually remained stationary for a time and then curved in toward the cut face and toward the branded side. This, however, is easily understood through the tissue tensions. Since the cortex with ordinary growth tends to lengthen much faster than the axial cylinder, the cortex of the concave side might lose much of its positive tension and still be longer than the axial cylinder. The decreased tension on the concave side would allow the tension of the convex side to curve the whole root, even if the tension on the convex side did not increase. But if, under these circumstances, the root was split into halves, the concave half would stop curving, and if the tension on the concave side had not been neutralized or reversed, this half could even reverse its curve; that is, curve in toward the cut face.

Table XI alone might seem to show that the concave side was the more active in producing the curve. We could not escape this conclusion if the curve were produced by the aggregate of the tendency of each individual tissue to curve. But recalling what we know of previously existing tissue tensions, we find it in complete harmony with the conclusion previously arrived at, that the stimulus diminishes tension on the concave side, and increases it on the convex side. Table XI especially confirms the view that the tension on the concave side is diminished, as well as changed otherwise.

It is possible, however, that the cortex of straight uninjured roots has a tendency to curve more or less regularly one way or another. Table XII will show that this is not the case.

This table is designed as control for XI. The roots were not branded, and were sliced in the same way as those in table XI. Since there was no curve the plane in which the three strips lie was not constant in relation to the seedling. In

comparatively few of these roots did one side of the cortex pull away from the axis more than the other. Eighty-two and nine tenths per cent. of them kept the same relative positions with respect to the axis. In many cases the two parts of the cortex lay up close to the axis, both remaining straight. In others the two parts pull away from the axis at the tip, though they seldom curved away from it very much. The axis always remains straight. From this table it is seen that there is no tendency in the cortex of straight unstimulated roots to curve as the cortex of stimulated roots curves. We are justified, therefore, in the conclusion that stimulation is the cause of the curving effects in the latter, when the cortex is freed from the axial cylinder.

TABLE XII.

MEDIAN SLICE OF STRAIGHT ROOTS SPLIT INTO THREE STRIPS.

	In Water			In 10% KNO_3		
Date, 1897	Roots used	One side curves more than other	Both sides curve equally from axis	All parts lie up close together	Both sides stand out equally from axis	One side stands out, other lies close to axis
Jan. 14	5	1	4	3	2	
15	3	1	2	2	1	
19	6	4	2	2	1	3
20	1		1	1		
Mch. 20	10		10			
30	10		10			
	35	6	29	8	4	3
		17.1%	82.9%	53.3%	26.7%	20%

The second part of table XII shows the effect of plasmolysis on some of the roots used. The first two columns of that part show that, in 80 per cent. of the roots tested for this particular effect, there was no difference in the tendency of the cortex on opposite sides of the same root to curve away from the axis when completely plasmolyzed.

In these experiments was first observed a very interesting phenomenon. When a root with the three strips free to move independently is put into 10 per cent. of KNO_3, the two strips

of cortex often curve far out from the axis, then rapidly come back up to it. The movement takes place within a few seconds and can be followed by the unaided eye. Whether the cortex spreads or not, almost without exception, so far as the observations went, the two strips of cortex at first became considerably shorter than the axis. The latter shortens much more slowly than the former, but after five minutes it has become shorter than the cortex and so remains.

I can think of two reasons why the cortex plasmolyzes more rapidly than the axial cylinder. The many intercellular spaces in the cortex allow the plasmolyzing agent to reach the cells more rapidly in this tissue. At the same time the abundant protoplasm in the cells of the axial cylinder may offer a greater resistance to the exosmosis of water than the thin layer of protoplasm in the cortical cells.

TABLE XIII.

MEASUREMENTS OF CURVING ROOTS.

First half cm. of concave side.

Date 1897	Roots used	Became longer	Did not lengthen	Shortened
March 20	5	2	2	1
24	3	2	1	
25	5	2	2	1
April 16	6		5	1
17	6	5	1	
	25	11	11	3
		44%	44%	12%

This table shows that there is not merely a relative shortening of the concave side, but in almost half of the roots tested there was no growth in length at all on the concave side in the first 0.5^{cm} from tip, and in 12 per cent. there was an actual shortening in that part.

The roots were marked off with India ink, some in 1^{mm} spaces, some in 0.5^{cm}, and then branded. After the curve had made some progress they were measured again. The time varied from two to seven hours after branding, according to the

rapidity with which the curve took place. Only the first 0.5^{cm} was taken, because within the time stated the curve is confined almost exclusively to that region of the root. By taking the average of the roots tested, it was found that there is a greater difference between the lengthening of the concave side and that of normal straight roots, under the same conditions, than between the lengthening of the convex side and that of normal roots. In other words, the relative shortening of the concave side is greater than the relative lengthening of the convex side. This is further evidence against the supposition that the concave side is merely compressed. It has previously been mentioned that numerous observers have found a shortening of the concave side in stems of both monocotyledonous and dicotyledonous plants.

In the early stages of the curvature the zone of maximum curvature does not coincide with the zone of maximum growth. Indeed the curve may be completed before the two coincide. This fact had been frequently noticed in many experiments, and twelve roots were observed with this especially in mind. From four to seven hours after branding, ten of the twelve showed the curve almost wholly in the first 0.5^{cm}, while the maximum growth of these same roots was in the second 0.5^{cm} from tip. Of thirty-one straight roots carefully measured, the two measurements being four hours apart in most of them, four showed a greater growth in the 0.5^{cm} nearest the tip, twenty in the second 0.5^{cm} from the tip, and seven grew the same in both half centimeters. Within twenty four hours of the time of branding, however, if growth continues, the zone of maximum growth meets the zone of maximum curvature and finally passes it. I suspect, but have not proved, that this is the time when many of the curved roots tend to straighten. These results agree with those of Wiesner (**78**, p. 233).

RELATION OF CONCAVE CORTEX AND AXIAL CYLINDER.

A few roots were bent forcibly with the hand for about ten minutes and after lying a few minutes free in water they were

sliced into the three strips as before. A considerable curve remained after the roots were freed from the bending force, and by measurement the convex side lengthened about 1^{mm}, and the concave side shortened about 1^{mm}. The shortening was of course all due to forcible compression, and yet after separation of the tissues, the cortex on the concave side, both in water and in 10 per cent. KNO_3 was somewhat longer than the axial cylinder. The cortex on the convex side was much longer than the concave cortex or the axial cylinder. This seems to make it rather improbable that the compression to which the concave side of the root may be subjected when it curves in response to a stimulus is sufficient to make the cortex shorter than the axial cylinder. Consequently when the cortex of the concave side does become shorter than the axial cylinder, as was found to be the case in some of my experiments (table VII), it must be explained on other grounds than passive compression. That there is such a shortening of the cortex on the concave side in its relation to the axial cylinder is shown by experiments performed by Sachs (**62**) and Ciesielski (**5**), who found that when the root is split into halves and the half root is placed in a horizontal position with the cut face upward, the half root sometimes remains straight, sometimes curves upward and sometimes curves downward; whereas, if the half root is laid with the cut face turned downward, the curve is invariably downward. It has already been noted in this paper (page 32) that when roots are split after they have begun to curve away from the brand on one side of the tip and the halves have been placed in an upright position, the curving of the concave half root toward the cut face is delayed, though it usually takes place later. The stimulus of burning one side of the root is a strong stimulus but applied for only a short time, and when the reaction from the effects of the stimulus sets in there is no further stimulating effect. When roots are laid in a horizontal position, however, the stimulus is continuous and its effects therefore are cumulative so long as the root tips do not attain a vertical position. For this reason the stimulus of gravitation is

preferable to that of injury for showing the effect of stimuli on the relation of axial cylinder to the cortex on the concave side of the curving root. I have therefore used gravitation as the stimulus in the following experiments. Seedlings of *Cucurbita Pepo* with roots 5–20^{mm} long were placed in a horizontal position in moist air, and when the curve had begun to show or before, the roots were split in the growing region and the upper or convex half of the tip was removed. For control observations roots were left whole or the lower half of the tip was removed. Thirty-four roots with one half of tip removed were placed in a horizontal position in moist air with the cut face upward. In two to four hours ten had curved slightly upward, six had curved slightly downward at tips, the others, eighteen in number, remained straight. In six to eight hours fifteen had curved more or less upward, eight downward, and eleven still remained straight. After twenty-four hours eleven were curved upward, and eighteen were curved downward.

As control for these, thirteen roots were laid in a horizontal position without injury. They all turned downwards within six to eight hours. Also seventeen roots were split and laid horizontal with cut face down. They likewise had all turned downward within six to eight hours, and some of them had formed a curve of 90° within two hours. There was, therefore, a very remarkable difference between the behavior of those roots which had the cut face of the split tip turned down and those which had the cut face turned up. While the former began at once to curve in toward the cut face, and the curve was completed rapidly, the latter nutated up and down for some time, and even at the end of twenty-four hours after splitting it was still undecided in which direction some of them would curve. In the thirty-four roots observed a larger number at first started to curve upward, and a few continued to curve in that direction. Others of this number later reversed the curve and finally turned downward. They sometimes showed a double curve, the split part farthest from tip turning up, but nearer the tip turning down. The same root often nutated up and down several

times before the direction of the curve was finally determined. At the end of twenty-four hours more than half were turned down at the tips, some of these tips being in a vertical position, others only slightly below the horizontal. This behavior indicates beyond doubt that there is a shortening of the cortex in relation to the axial cylinder on the side of the root that becomes concave, for in these roots with the upper half of the tip removed there can be no compression of the cortex on the lower side by the increased growth or extension of the cortex on the upper side, and the normal tension between the cortex and axial cylinder of a half root is such as to cause it always to curve with the cut face concave. It has already been shown that a half root stimulated on the outer side of the tip curves with the cut face concave not only more rapidly than a whole root so stimulated, but also more rapidly than an unstimulated half root (*fig.* 1). We are forced to the conclusion that a stimulus to the root increases the tissue tension between axial cylinder and the cortex on the side that becomes convex, and decreases or reverses the tension between the axial cylinder and the cortex on the side that becomes concave. These changes on the opposite sides of a curving root are independent of each other, and neither side of the root is passive in the curvature, but both are active in producing it. Those theories, therefore, which attempt to account for the curvature by a change on only one side of the root, whether on the convex or concave side, cannot be accepted.

I have made numerous attempts to find a difference in the turgor of cells on the concave and convex sides of the curving root, but was not able to demonstrate such a difference. Solutions of KNO_3 of varying strength were used, and the two sides always plasmolyzed in the same solution and in the same time. In a few cases it was noticed that the cells of stimulated roots plasmolyzed with a weaker solution than straight uninjured ones that had been under precisely the same conditions. The point was not pursued far enough to show whether or not the difference was merely an individual variation.

MEASURING CELLS.

In measuring cells in *Vicia faba* roots it was found that in those which were strongly curved, most of the cells of the cortex on the concave side between the zone of the greatest curvature and the tip had their radial diameter longer than the diameter parallel to the long axis of the root. This is true to about 3^{mm} from the tip of strongly curved roots, but beyond that point the cells elongate rapidly, so that the radial diameter becomes shorter than the one parallel to the long axis of the root. The fact that the cells in the region mentioned have the radial diameter greater than the other is positive proof against Kohl's contraction theory as applied to these roots. Any contraction necessarily takes place partially in this region, and according to Kohl's theory the increased turgor shortens the longer diameter of the cells on a concave side. It is inconceivable, however, that the longer diameter could become the shorter one through increased turgor. Since the cell diameter parallel to the direction in which the cells are supposed to shorten is less than the diameter transverse to that direction after the curve is produced, it is obviously impossible for the shortening of the concave side to be brought about as Kohl supposed. In the discussion of grass nodes Kohl himself writes (**33,** p. 49): "The transverse diameter of the concave cells is greater than the longitudinal diameter." But Kohl evidently did not see that this condition invalidated his theory of curvature.

WATER CONTENT OF CONVEX AND CONCAVE SIDE OF CURVING ROOTS.

In a series of experiments I have determined that there is a greater relative amount of water in the convex half of curving roots than in the concave half, but this is just what should be expected if we take into consideration the enormously large vacuoles on the convex side as compared with those on the concave side. As I do not consider these results of very great importance, I shall not give them in full, but only a summary.

The method was as follows: roots were branded as usual, and after the curve had made considerable progress, the roots

were separated into two lots, one for the control of the other. The average time was about six hours after branding, and the extreme limits were 3.5 and 11.5 hours after branding. In the control experiments the roots were taken from water and the outside carefully wiped with a dry cloth to get rid of the water adhering to them, and just enough of the tip was cut off to take in all the curve. These tips were put into a weighing flask, which was closed air tight. In the other experiments the roots were split into two parts as nearly equal as possible, one half being the concave, the other the convex side of the curve. The two halves were cut off by a cut transverse to the root at the point of cutting, and just enough taken to include the whole curve. The convex halves were put into one flask, the concave halves in another. The flasks had all been previously weighed, now the weight of the roots was ascertained. They were then dried quickly at a temperature of 100° C. until they ceased to lose weight, and were weighed again. The loss in weight, which equals the amount of water, was calculated on the basis of the fresh weight.

A total of 143 roots were split and seventy-three were taken without splitting. The control and the split roots were weighed in fourteen different lots of each. With the exception of one lot they all showed a greater percentage of water in the convex halves than in the concave halves. That one exception was the one in which the time was the shortest, and the excess of water in the concave side was only 0.07 per cent. In the other lots the extreme limits of variation were 0.08 per cent. and 1.9 per cent. in favor of the convex side. The total amount of water varied from 87.42 per cent. to 91.93 per cent. in the convex side and from 87.49 per cent. to 90.86 per cent. in the concave side. In the whole tips the variation was from 85.96 per cent. to 91.15 per cent. One third of the lots of the latter showed a greater amount of water than the corresponding split roots. One third were between the convex and concave sides of the corresponding split ones, and one third fell below the concave side in the corresponding lots.

Another series of control experiments was used in which straight roots were split into halves, and the water content of the separate halves ascertained as before. The stimulated roots were all branded on the side of the tip facing the hilum of the seed, so that side was always the convex side of the curve. The straight unstimulated roots were always split in the corresponding plane and a record kept as to which was the side next to the hilum. So the two series were exactly comparable. The lots were nearly all treated at the same time and under exactly the same conditions as the curved ones. A total of fifty-nine straight roots were split and weighed in six different lots. The variation on the side next the hilum, corresponding to the convex side of the curved roots, was from 87.72 per cent. to 92.51 per cent., and on the opposite side from 87.63 per cent. to 92.49 per cent. In three lots the excess was on the hilum side and in three lots on the opposite side.

Nothing has been proved as to the absolute increase or decrease of the water content in stimulated roots, but it is shown beyond a reasonable doubt that there is a relative increase of water in the convex side of curving roots. This does not prove, however, that the greater amount of water on the convex side increases the size of the cells. It may simply mean that the increased size of the cells enables them to hold more water with the same turgor pressure. Indeed, the increased amount of water must necessarily reduce the concentration of the cell sap and therefore the osmotic pressure, unless there is at the same time an increase in the production of osmotic substances in those cells. I know of no evidence for such an increased production of osmotic substances, and Kraus has shown that there is a relative and absolute decrease in osmotic substances on the convex side during the later stages of the curve. My results agree with his as to the increase of water on the convex side.

SUMMARY OF EXPERIMENTS.

The experiments submitted justify the following conclusions:

1. The transmission of the stimulus from the sensitive tip to that part of the root which curves takes place in the cortex. It may take place in the cortex of either the side that becomes concave or that which becomes convex, and is not restricted to the side on which the root tip is wounded.

While it is not absolutely demonstrated that transmission cannot take place in the axial cylinder the evidence is strongly against such an assumption.

2. The stimulus may be transmitted in the transverse or tangential direction as well as in the longitudinal direction.[4]

3. The mechanism of root curvature, as in curvature of stems, is closely connected with the tissue tensions existing in the organ previously to stimulation.

4. The ordinary tissue tension of roots is the reverse of that in stems. That is, the outer cortical parenchyma is under positive tension, the central cylinder under negative tension. Three lines of evidence show this to be true; first, the rupturing of the central tissue in rapidly growing roots; second, the curving in of split roots with the cut face concave; third, the difference in length of the cortex and axial cylinder when separated from each other. It is not uncommon in *Vicia faba* roots for this difference to be as great as 10 per cent. of the length of the separated tissues, when the separation is for 1 cm back from the tip.

5. Stimulation causes an increase of the tension between the axial cylinder and the cortex on the side which becomes convex, and decreases or reverses the tension between the axial cylinder and the cortex on the side that becomes concave. The shortening of the concave side may be merely relative or there may be an absolute shortening as has been shown by Kohl and myself. That the shortening is not due merely to compression by the more rapid extension of the cortex on the convex side is proven by the behavior of split roots that are laid in horizontal position

[4] A recent article by Ewart (20) shows that in the climbing hooks of various tropical plants the stimulus is transmitted in a transverse or tangential direction from the concave side, which alone is sensitive to contact, pressure, and injury, to the cambium which is incited to increased growth.

with the cut face upward. The up and down nutation exhibited by roots in that condition can only be due to the varying tension between cortex and axial cylinder in the half root that becomes concave; and the fact that more than half of the roots experimented upon in that way finally curved downward proves that the tension may be often reversed in the concave half of the root. This conclusion is also indicated by the relative length of the separated tissues of curved roots, though in these cases compression of the concave cortex is not eliminated. Experiments similar to those just mentioned, but with different details, prove the increased tension on the convex side.

6. Not only is the tension between the axial cylinder and the cortex on the side that becomes concave changed by the stimulus, but the different layers of the cortex itself change in their tensile relations to one another. In curving roots the outer layers of the cortex on the concave side are under negative tension in relation to those layers lying more central. This is shown by the fact that when the tissues of curving roots are separated the concave cortex curves more than the whole root has done, often curving with a sudden jerk as soon as separated, and forming a curve with a very short radius. That this is not due to the normal tension of the epidermis and root cap is shown by comparison with the convex cortex and with the isolated cortex of unstimulated roots. It is not impossible that forcible compression of the outer layers of the concave side may sometimes play a part here. Such compression necessarily takes place in the outer layers of this side notwithstanding its shortening, unless the outer layers are shortened more than the inner ones as a direct result of the stimulus. If the greater shortening of the outer layers was merely the result of compression, we should expect them to lengthen when freed from that compression, and the isolated cortex would then straighten. Since the isolated cortex curves more strongly than before isolation, it seems probable that the change produced directly by the stimulus in the cells of the concave side is greater in the outer layers of that side than in the inner layers.

Mo. Bot. Garden,
1900.

The root reacts to the stimulus as a whole, and is not affected merely on one side. The changes in the cells of the two opposite sides, which become respectively concave and convex, are opposite in their effects, and these changes are coordinated so as to bring about the curvature with a fairly economical expenditure of energy, so far as this is indicated by the tissue tensions. It is remarkable that a stimulus may be transmitted in one side of the cortex past a deep gash in the opposite side, and yet above the gash produce opposite effects on the opposite sides of the root. The mechanism of the curvature is a more complicated problem than some writers on the subject have imagined.

7. In the traumatropic curvature of *Vicia faba* roots, the zone of maximum curvature does not coincide with the zone of maximum growth, but is nearer the tip. In four to eight hours after the beginning of the curve, it is mostly in the first half-centimeter from the tip, while the greater growth during the same period is in the second half-centimeter from the tip. Within twenty-four hours, however, the zone of maximum growth meets and may even pass the zone of maximum curvature.

8. The proportions of cells in the curving part of Vicia roots are such that Kohl's theory of the curvature cannot possibly be true for them.

9. The cells of the convex half of curved roots contain a larger quantity of water than those of the concave half.

Theoretical considerations.

After examining carefully the experimental evidence we are forced to the conclusion that no theory yet advanced is adequate for the explanation of all curvatures due to stimulation. Sachs' earlier view that there is merely a difference in the rate of growth on the opposite sides of the curving organ does not explain satisfactorily the contraction often observed on the concave side; and even if it did explain this contraction it would not be a complete explanation of the curvature, because we do not yet know what growth really is; nor do we know the immediate source of the energy of growth. The evidence is against de Vries' view

that there is an increased turgor on the convex side of the curving organ. Wiesner's view that when the root tip is injured on one side the cell membranes on that side above the wound are made more extensible, does not account for the changes on the opposite side which are indicated by my experiments. Wiesner makes a distinction between geotropic and traumatropic curvatures. In the case of the former he supposes an increase of ductility of the cell membranes on the side becoming convex, and also an increase in the elasticity of the cell membranes on the side which becomes concave. Even though we admit that a sufficient increase in the elasticity of the membranes on the concave side could shorten the cells by forcing water out through the protoplasm, we may well doubt whether that is the method by which the cells are shortened, until further evidence has been presented in favor of that view. We must believe that the elasticity of the membranes is brought about only by the activity of the protoplasm; and it does not seem to be an economical expenditure of energy for the protoplasm to increase the elasticity of the walls until their pressure forces water out through the protoplasm, when by its activity it can change its permeability to water and allow the cells to shorten without increasing the elasticity of the cell walls. It has already been shown (p. 44) that the concave side shortens in relation to the axial cylinder when compression by the cortex of the convex side is out of the question.

Nöll supposed he had proved the greater extensibility of the membranes on the convex side of curving stems by his bending experiments. With the same pull the stems bent more toward the concave than toward the convex side. It has been shown (p. 26) that this is the necessary result of the tensions in stimulated stems; therefore it is evidence only of those tensions, and not at all in favor of any particular method by which those changes from the normal tension are brought about. Noll showed by other methods that the size, and the optical and staining properties of membranes on the convex side were different from those of unstimulated stems; and it may be that the

membranes on that side are really more extensible than those of normal stems. My own experiments show that the convex half of the stimulated roots which are split when the curve begins, curve much more rapidly that the similar half of unstimulated roots; and to that extent my experiments may be said to support the view that the convex side of stimulated organs is more extensible than similar cells of normal organs. But that this is the only factor, or even the main one, in the curvature of stimulated organs is disproved by the experiments of Sachs and Kohl for stems, and my own experiments on roots, which show that in both stems and roots changes also take place in the concave side of an opposite kind from those in the convex side. Enough has been said to show that MacDougal's conclusions as to the mechanism of root curvature cannot be accepted as adequate.

Since the theories of Wortmann, Kohl, and Loeb all regard the concave side as alone active in the formation of the curvature, they are inadequate at the best. They take no account of the decreased tension in the convex side of curving stems, and the increased tension in the convex side of curving roots. Wortmann's theory also fails to account for the contraction of the concave side. Moreover, objections have been made to it by Noll, Kohl, and others which remain unanswered, and probably are unanswerable.

Aside from the inadequacy of Kohl's theory as a complete explanation of the curvature, it is not even proven as the cause of contraction of the concave side. While theoretically possible, perhaps, it requires that the cells in the region of curvature have their longer diameter parallel to the longitudinal axis of the curving organ. Kohl's own work shows that this condition does not exist in grass nodes, and my observations show that it does not exist in the tip half of the curved zone of *Vicia faba* roots. Moreover, Kohl's theory would seem to require that at the beginning of plasmolysis the cells of the concave side should lengthen, and the curve be somewhat straightened; but Kohl and Noll both found an increase of the curvature at the beginning of plasmolysis, when the curve was not too old.

Loeb seeks to explain the contraction of the concave side in curving plant organs by the same process as the contraction of animal muscle. He states that in an active muscle there is an increase of osmotic substances, and that a weighted contracting muscle takes up more water than a resting one. He points to the observations of Kraus as proof that osmotic substances are increased in the cells of the concave side of curving plant organs. He offers no proof or evidence, however, that these cells take up more water than the cells of the convex side. Indeed all the evidence is against it. My weighing experiments with the concave and convex halves of curving roots prove beyond doubt that the convex side contains more water than the concave side. Hence the contraction in plant cells cannot be the same as in animal cells. Pulvini also show a loss of water in the cells of the contracting side. Loeb does not consider sufficiently the contracting power of the elastic membranes of turgid plant cells, which may contract with a decrease of osmotic pressure.

When we consider the varied mechanical conditions which are found in such plant organs as fungus hyphæ, grass nodes, dicotyledonous stems, and roots, we should hardly expect, even *a priori*, that a single explanation of curvature would apply to all plant organs. How much less should we expect that a single explanation would apply not only to all plant curvatures but also to contractions of animal muscles, and to free movements of both plants and animals, as Loeb would have us believe. The experimental evidence is against this view.

Pfeffer has shown that in grass nodes the curve is brought about by an active growth of the collenchyma bundles of the convex side. Even here a certain amount of potential energy, which exists previously to stimulation in the form of the positive tension of the parenchyma, becomes available for growth of the collenchyma. In their growth the walls of these collenchyma cells undergo those changes which Noll says indicate plastic stretching and greater ductility of the membranes. That the walls are more ductile may be admitted and the ductility still be

regarded as a phenomenon of growth. Similar changes in the membrane have been shown by Strasburger to accompany growth in the formation of new branches of Cladophora. Whether the shortening that has been frequently observed on the concave side of curving grass nodes is due to compression merely or to active shortening has not been demonstrated.

The climbing hooks of various tropical plants investigated by Ewart in Java (**20**) are examples of organs which respond to stimuli by increased cambial growth and cell division. Here also the mechanical relations of the tissues are such that neither mere changes of turgor on opposite sides nor any plastic or elastic stretching could produce the response to stimuli which these organs show. The curve of the hook may be increased by a greater growth on the convex side; or the hook may be made to clasp a support merely by an increase in the transverse diameter which diminishes the diameter of the circle already formed by the normally curved hook. In either case the response takes the form of growth.

Noll has reported experiments with Hippuris stems which are perhaps of more importance than he supposed (**50,** p. 51). The stems were laid in a horizontal position in air not saturated with moisture and they were not in contact with liquid water. Nevertheless they curved upward in a U-shape; and the lower convex side was smooth, shiny and turgid, while the upper concave side became wrinkled and limp. Since the stem could get no water from the outside, any increase in the amount of water in the cells on the lower side must have come from the cells on the upper side. The water could not have been forced out of the cells on the upper side by mechanical pressure from the lower side, because that pressure could have been exerted only after the lower side had obtained more water. Either the cells on the lower side withdrew water from the cells on the upper side by a greater osmotic power, in which case the water would not pass into the intercellular spaces; or the cells on the upper side, affected directly by the stimulus, allowed the water to pass into the intercellular spaces, and the water was then taken up by the

cells on the lower side. I see no other alternative. Greater extensibility of the membranes on the lower side could not enlarge the cells unless they took up more water. The evidence is against the greater osmotic pressure on the lower side; and the conclusion seems inevitable that the cells on the upper side, from the immediate effect of the stimulus, allowed water to escape into the intercellular spaces. This could be brought about either by increased elasticity of the walls or increased permeability of protoplasm to water. From what we know of effect of stimuli on other plant organs, the latter view seems more probable, though it is possible that both the elasticity of the walls and the permeability of the protoplasm are increased by the stimulus. If the stimulus can cause the cells on the upper side of a horizontal Hippuris stem to give out water into the intercellular spaces as a direct effect, we are justified in thinking that the shortening of the concave side in other stems and in roots also can be brought about in the same way. Noll has observed that when curving stems have been gashed on one side, water is gradually forced out of the gash, and shows in the form of drops. The water must have come from the intercellular spaces into which it had escaped from the cells on the concave side.

MacDougal asserts (**39,** p. 309) that there are no intercellular spaces in the motor zone of roots into which water could pass from the cells. He is certainly mistaken as regards *Vicia faba* roots in which well developed intercellular spaces are found in the cortex very near to the initial zone. In sections from fresh roots their presence is easily demonstrated by the air contained in them. MacDougal himself, however, says in another place (**39,** p. 309) of the roots of *Zea mais*: "Intercellular spaces (of the convex side) are larger and more abundant than in the concave side." Evidently there are intercellular spaces in roots of Zea also. This makes the condition favorable for water to escape from the cell if the protoplasm becomes more permeable. That the stimulus produces this condition in roots has not been proved; but it seems to me to be the most reasonable explanation of the phenomena exhibited in the concave side of curving

roots. The loss of water due to greater permeability of the protoplasm accounts for the decrease or the reversal of the tension between the cortex and axial cylinder on the concave side; and it is especially satisfactory in explaining the actual shortening of the concave side which has been so often observed by different men in grass nodes, dicotyledonous stems, and roots. In answer to the objection that mechanical compression may also shorten the concave side, I have already shown (p. 44) that there is at least a relative shortening of the concave side under conditions where compression cannot possibly be exerted by the convex cortex in the case of roots; and Noll's Hippuris stems show the same thing for dicotyledonous stems. The objection that greater elasticity of the cell membranes may cause the shortening is answered on p. 51; but this elasticity is not excluded absolutely as one of the factors in the curvature.

Noll has pointed out that in wilting plants the cell sap may become more concentrated and its osmotic equivalent greater while turgor falls; hence the greater permeability of the protoplasm in the cells of the concave side is not contradictory to those observations of Kraus and Kohl which show an increased amount of osmotic substances on the concave side. Indeed it may be that the very activity by which the protoplasm becomes more permeable results in an increased production of osmotic substances, as Vines has pointed out.

The loss of water through greater permeability of the protoplasm on the concave side is not disproved by the fact that the concave side often lengthens more or less during the curvature. Turgor might sink quite appreciably from the loss of water and the cells still be capable of growth in length; and in those cases which lengthen, this growth more than counteracts the shortening effect. If the cells did not grow in length the walls could still grow in thickness, and the thickened walls observed by Wortmann are thus accounted for.

The time required for root curvatures cannot be regarded as evidence against the increased permeability of protoplasm in them, for MacDougal has found that tendrils coil in response to

contact by allowing water to escape from cells on the concave side, and the reaction may take as long as 1⅔ hours (**38,** p. 376). Roots often curve 90° within two hours.

The shortening of the cells on the concave side by allowing water to escape is also in harmony with the results of Noll's bending experiments, since, as I have previously shown, those results are merely the expression of the tissue tensions in stimulated organs, and indicate nothing as to the particular method by which those tensions are produced.

It has already been mentioned that Noll and Kohl both found, in the early stages of the curve, an increase of the curve on first putting the organ into a plasmolyzing solution, and this plus curve was followed only later by the straightening of the organ. Each of these men claimed that the plus curve was in harmony with his theory of the curvature; but the criticism of Noll's argument compelled him to admit that the problem was more complex than he had supposed and that he had not explained the plus curve. I am totally unable to see the logic in Kohl's argument, or to see how his theory explains the plus curve at the beginning of plasmolysis. On the other hand it seems to me easily explainable on the theory that the protoplasm in the cells of the concave side becomes more permeable to water. If we suppose that the protoplasm becomes more permeable by an increase in the size of its molecular interstices, then a given amount of energy, whether exerted by the elasticity of the cell walls or by a plasmolyzing solution outside of the cell, will withdraw a given amount of water from the cell *in a shorter time*. Hence when a curving root or stem is placed in a plasmolyzing solution a plus curve necessarily follows at first, if the protoplasm of the concave cells is more permeable; but while the convex side plasmolyzes more slowly, since its protoplasm is less permeable, the cells on that side finally shorten more than the cells on the concave side, and the end result is a straightening of the whole organ.

Some observations of Kohl seem to contradict the view that the cells on the concave side plasmolyzed more rapidly than on

the convex side. Kohl says he found constantly that the protoplasm in the cells of the convex side pulled away from the cell wall sooner than in the cells of the concave side. If there is a real contradiction here it is not so much between Kohl's observations and the greater permeability of the protoplasm in the concave cells as between the two series of observations made by Kohl himself, one showing that plasmolysis gives a plus curve at first, and the other that the convex cells plasmolyze sooner. There appears to me a possibility however, that makes the contradiction only apparent and not real. MacDougal found in tendrils which were plasmolyzed, then fixed and cut into thin sections, that the protoplasm of the cells on the convex side was pulled completely away from the wall, while in the outer rows on the concave side it was barely separated from the wall. Nevertheless the tendril, when plasmolyzed, had increased its curvature and MacDougal believes he has shown that the protoplasm becomes more permeable in the cells of the concave side. The explanation seems to me to be that the protoplasm becomes more permeable not only for water, but also for the plasmolyzing solution. Hence the protoplasm in the cells of the concave side allows the KNO_3 to pass inward to a greater or less degree, while that in the cells of the convex side resists penetration by the plasmolyzing solution, and on the convex side the protoplasm is forced away from the walls sooner and more completely than on the concave side. Some observations of my own seem to show that the protoplasm in the parenchyma of *Vicia faba* roots can become permeable to KNO_3. In numerous sections the protoplasm in the cortical parenchyma was not contracted from the walls even in a 10 per cent. solution, though the cells had completely lost their turgidity I was not able to see any difference in the pulling away from the wall of the protoplasm in the cases which showed that phenomenon, even when Kohl's method was used. My observations on that point were not extensive, however. Different observers have reported quite different results as to the plasmolysis of cells of the convex and concave sides, and the point probably needs

further investigation. On the whole, the view that the protoplasm in the cells of the concave side becomes more permeable seems to explain more phenomena than any other view yet advanced; and while it is not absolutely demonstrated, I believe it to be the condition which lies at the basis of those changes which, as my experiments show, take place in that half of a stimulated root which becomes concave.

As for the changes which take place in the half that becomes convex, there is certainly an increased growth on that side; and Noll has shown that there is in some cases a change in the quality of the membrane. It is not proved, however, that this change in the membrane is a condition preceding growth, as Noll believed, since it may be merely the method of growth. This point can be decided only when our knowledge of the mechanics of growth is more complete.

In the light of the foregoing experiments and arguments the mechanism of the curvature of roots is as follows: The stimulus is transmitted from the sensitive root tip to the curving parts, in the cortical parenchyma. The effect of the stimulus is to increase the normal tension between cortical parenchyma and axial cylinder on the side that becomes convex, and to decrease or reverse the normal tension between the cortical parenchyma and the axial cylinder on the side that becomes concave. The change in tension also extends to the different layers of the cortical parenchyma on the concave side, the outer layers becoming negative with respect to the inner ones. So much has been demonstrated. The evidence is in favor of the view that the tensions on the concave side are changed by the protoplasm becoming more permeable to water, some of which passes out into the intercellular spaces, possibly to be taken up by the convex cells, which later contain more water than the concave cells. The shortening of the concave side may be masked sometimes by a certain amount of growth.

The same explanation will apply to curvatures of dicotyledonous stems if allowance is made for the different normal tensions found in them.

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BRIEFER ARTICLES.

BOTANICAL BIBLIOGRAPHY.

THE announcement in a recent number of *Hedwigia* that, at the request of a number of subscribers, it is proposed to abandon the publication of bibliographical notices in that journal, except in a few cases, brings up the question of the best method of issuing notices of current botanical literature. The question is especially pertinent at the present time, since the publication of an international scientific catalogue is under discussion. Those who have expressed their views on the subject have considered principally two points, viz., (1) whether the proposed catalogue should be a card catalogue or should be issued in some other form; and (2) the best classification of subjects to be adopted. In this country the card catalogue is generally preferred. It is not necessary to discuss here in detail the merits and defects of such a catalogue so far as it is to be used in large public and university libraries. In a certain sense, however, all working botanists may be said to be librarians on a small scale, and the question which concerns us is, how shall we best secure a good record of current literature for our private use? Probably most botanists have card catalogues of subjects in which they are most interested, but such catalogues must be made by individual botanists, each from the standpoint of his own particular needs, and they could not be furnished wholesale by any publication agency.

What botanists want is a list of the titles of botanical publications as soon as possible after their issue, together with such accounts of their contents as will enable them to determine whether they need to buy the publications named, or to recommend the libraries near at hand to buy them. This information in a very large number, if not in most, cases cannot be given on any card of the size proposed for use by those who advocate card catalogues, and a card catalogue, valuable as it is in many ways, cannot be transformed into what is wanted, viz., a series of short descriptive, not critical, reviews. To accomplish the important object of furnishing botanists as speedily as possible with adequate notices of current works, it seems to us better to utilize some

regular botanical journal under competent management, with a numerous staff of editors, than to depend on a general international scientific catalogue, whether issued in the form of cards or printed sheets to be bound together. Just's *Jahresbericht* is probably as good a work as is practically possible except in the delay of publication, which probably might be reduced by skillful management so that it would be only a year behind the time. In a journal which should have for its sole object the publication of notices of current literature, the delay of a year would be fatal; but, in order that the notices might be up to date, it is plain that it would not be possible to treat the material with the same thoroughness and completeness as in Just's *Jahresbericht*, where time is taken to digest it thoroughly. In the case of a journal reviewing current literature we can only ask that the notices shall appear as quickly as possible and that the whole ground shall be covered as far as is practically possible, expecting that some works will escape notice at the time.

The form of journal which it seems to me is best adapted for the purpose is something like that of the *Botanisches Centralblatt*, and the question arises, would it be possible to transform that journal so that it might become a satisfactory organ to be accepted by all botanists as the standard record of current literature? We may therefore, in the interests of those desiring as satisfactory a journal as possible for the record of current literature, offer certain criticisms on the *Centralblatt* as now conducted, not, however, intending to reflect on the management of the journal, which deserves praise for its activity and enterprise. At present, the *Centralblatt* furnishes original articles, reviews of recent books and papers, and a list of current publications, besides certain items coming under the head of news. It may be said with truth that by far the larger portion of the subscribers take the *Centralblatt* for the sole purpose of knowing the contents of botanical publications as soon as possible after their issue. They do not take the journal because they expect to find in it important original articles, but they do expect, in return for their money, as complete an account of current literature as the editors are able to furnish. Since 1891, however, it has been the practice of the *Centralblatt* to issue a series of *Beihefte*, forming annual volumes of about 500 pages, not included in the subscription price of the journal but issued as independent volumes. The result is that one is practically forced to pay two prices in order to obtain the complete set of notices; the notices which one would care to

have are quite as likely to be found in the *Beihefte* as in the *Centralblatt* itself. The great body of subscribers are practically paying for what they do not want, the original articles, and are forced to pay an extra price for what they do want. It would be quite possible, by omitting the original articles or relegating them instead of the notices to the *Beihefte*, to include all the notices in the four regular volumes issued annually. Certainly this result could be accomplished if the lengthy notices of certain works not of primary importance were condensed as they should be, the interest of the reader being consulted rather than the wishes of the author.

On looking over the original articles in the *Centralblatt* it will be seen that, while a certain number are important, they are almost always short, and, it must be confessed, not numerous; on the other hand, the majority, it can hardly be denied, are tedious and on subjects which could interest very few readers. A good share of the original articles would appear more properly in the proceedings of learned societies than in a current journal. Again, the subscriber hardly cares to pay for polemic tirades of a personal and perhaps undignified character.

We are, of course, speaking in the interest of the subscriber. As far as the interests of the publishers are concerned the following suggestion may be offered. If, by suppressing the original articles and limiting the journal to the one object of furnishing notices of recent works, avoiding lengthy notices of the less important and rejecting those containing personal criticism, the journal could be generally recognized as an indispensable record of current literature, would not the number of private subscribers be so much increased as to more than counterbalance the subscriptions now received for the *Beihefte?*

As it is, the *Centralblatt* is a valuable journal, and, with certain modifications which seem to me practicable, it would become so nearly perfect, practically speaking, that for the purposes of botanists it would be better than any international catalogue and could be sold at a price not beyond the means of most working botanists who would find that they could not do without it; whereas now they hesitate to subscribe to the *Centralblatt* because they know that for many of the notices they will have to subscribe for what is practically another journal. If it is not feasible in the opinion of the publishers of an existing journal to transform it into such a record of current literature as is desired by botanists, the question arises whether, by a combination among

botanists, it would be possible to issue such a journal directed by a number of capable editors who should receive pay for their services, it being understood, however, that such a journal would pay its way without leaving a profit. To secure a good result, it seems to be necessary that certain competent persons should be paid for writing the reviews. Gratuitous notices written by the authors themselves cannot be depended on, for authors are given to prolixity in reviewing their own works. In a recent *Beiheft* of the *Centralblatt* is a review covering twenty-five pages, written by the author himself! In this case a single page would have answered every purpose and it would have been cheaper to pay someone to write that page than to pay for the printing of twenty-five pages.

As a last alternative, if no other arrangement can be made, the following tentative experiment might be tried. By private subscription a sum might be raised to establish a journal which, for five years, should give the record of botanical literature in a single country, our own for instance. The experiment might be worth trying, and, at the end of five years, if the experiment proves successful, the journal could be made to cover a larger field on an independent footing. If unsuccessful, it could be abandoned, probably without much loss.— W. G. Farlow, *Cambridge, Mass.*

CURRENT LITERATURE.

BOOK REVIEWS.

A text-book of botany for students of pharmacy.

THIS book, by Drs. Rusby and Jeliffe, is really a second edition, the first being issued under the title of *Essentials of Pharmacognosy*. The present work[1] is greatly enlarged and greatly improved. Part I by Dr. Rusby treats of vegetable organography. The drawings are original and for the most part very good. The subject-matter is treated with great care and with a special view to its didactic purposes. A criticism that may be offered is that too many definitions and explanations of unusual and trivial botanical terms are given. This criticism seems especially applicable in consideration of the fact that botany in colleges of pharmacy must be presented in an elementary way. It does not seem advisable to load the mind of the student with definitions of terms which are self-explanatory, or which may never be used. Some of the definitions are confusing because of a lack of proper coordination and subordination of terms. This defect is apparently not due to carelessness, but due to a difficulty in coming to a decision as to what should be coordinated and what should be subordinated. The cryptogamous plants are treated in a very elementary and somewhat antiquated manner, defects which we hope may be remedied in subsequent editions.

Taken as a whole, Dr. Rusby's part possesses many commendable features and we believe it to be the best book of its kind by an American author.

Part II, Vegetable Histology, by Dr. Jeliffe, is a great improvement upon the former edition, but there is much room for further improvement. The subject-matter is presented in rather an erratic manner. The author should also observe greater care and accuracy in making statements. For example, the cell is said to be "the unit of structure as well as the unit of physiological activity," which is an antiquated idea. Again, the author states that "animal tissues are in general characterized by the slight development or absence of cell walls," which is not exactly in accordance with facts. Under the discussion of protoplasm "four prominent theories" of protoplasmic structure are mentioned: (1) "The granule theory; (2) the reticulum theory; (3)

[1] RUSBY, H. H. and JELIFFE, S. E.: Morphology and histology of plants, designed especially as a guide to plant-analysis and classification, and as an introduction to pharmacognosy and vegetable physiology. Part 1. The morphology of plants, by H. H. Rusby. Part I. Plant histology, by Smith Ely Jeliffe. 8vo. pp. xii + 378. *figs. 693*. New York: The Authors. 1899. $3.00.

the foam theory; and (4) the filar theory." These are not true theories and the very misleading and defective statements of them will only convey erroneous ideas of the really grand cytoplasmic studies of Altmann, Bütschli, Strasburger, Wiesner and others. The author states that the "cell can live without cytoplasm, but without a nucleus it is devoid of the power of growth and repair," a startling statement even to the layman, in consideration of the fact that on the opposite page it is stated that "cytoplasm is the seat of the active life processes of the plant." It is quite evident that the defects cited and many others are largely due to carelessness rather than a lack of information.

The illustrations are good, being carefully selected from the works of various authors. There are also good original illustrations. The citation of authorities is of great value to students who have the desire and opportunity to do collateral reading.

The book is well made, with good type, paper, and fairly good binding. The index is very complete, but we regret that it is in two parts.

A text-book of botany fully adapted to the needs of students of pharmacy is not yet produced, but the authors are to be congratulated upon having produced a text which meets the requirements better than any other book upon the market. — ALBERT SCHNEIDER.

By way of supplement to the above it needs to be said that Dr. Rusby's part of the book does not depart from the usual type of books, in vogue twenty years ago, intended to "prepare" the student for "plant analysis." Twenty-seven pages are given to the cryptogams, which is too little for adequate presentation even in the most elementary way, and too much to be wasted. Sixty-seven pages are all that can be spared to the morphology of root, stem, and leaf, and most of this is purely formal; while almost 150 pages are devoted to the flower, fruit, analysis, collecting, nomenclature, etc. In this portion, also, the morphology is not modern, to say the least. Why assure a student that "a flower will obey certain well-defined laws" when the bulk of the chapters on the flower are concerned with explaining how they "disobey" these "laws" and in defining terms that are used to describe departures from a purely imaginary pattern? The whole treatment of the flower, indeed, proceeds upon the pernicious theory of metamorphosis.

When Dr. Rusby enters upon the attempt to present the idea of alternation of generations, beginning with spermatophytes, he essays a most difficult, if not impossible, task. His exposition shows that he has not understood the homology of some of the parts, and he has even misstated the process of fertilization. Indeed, whenever the author gets away from the terms necessary for phytography, in which he is an adept, he betrays a lack of familiarity with modern thought that is only too common among systematists, even the greatest. As an "introduction to analysis" the book may be useful, but as a "morphology of plants" it is open to the most adverse criticism. The old was better. — C. R. B.

The African flora.

OF ENGLER'S great work on the genera and families of African plants[2] the third fascicle has appeared, containing the synopsis of the Combretaceæ (17 genera, of which 10 are African) and the elaboration of the genus Combretum, by Engler and Diels. This family of the African flora is particularly interesting not only because it contains a large number of species of Terminalia and of Combretum (184 of the latter are here described, of which 78 are new), but because many of the species are strongly localized, with marked differences between the eastern and western types, and because of the complete absence of a natural grouping of the African species of Combretum.

For this monograph the authors have been able to lay under contribution not only the unrivaled collections of the Berlin herbaria, but also the rich African collections at Zürich, Rome, Brussels, Coimbra, Hamburg, and Kew. The work is beyond praise. Thirty elegant plates illustrate it. Since it includes not only a synopsis of all the genera of the family, but also a discussion of the distribution of the various groups, African and other, of the genus Combretum, the direct usefulness of this monograph will not be confined to those herbaria which include African plants. It will be indispensable to all taxonomic libraries.

WE HAVE previously noticed the publication of the *Illustrations* of the flora of the Congo, of which three fascicles with 36 plates have already appeared. This work is now accompanied by the first fascicle of a text entitled *Contributions a la flore du Congo* by Dr. E. de Wildeman and Th. Durand, listing the newly discovered species and describing new ones from that state.[3]

This contribution lists 344 species of phanerogams and ferns, bringing the number of known species from the Congo Free State to above 1500. Thirty-seven new species are described by Wildeman and Durand, Radlkofer, Pax, Cogniaux, and Stapf. One new genus, *Stironeurum* (Sapotaceæ), is established by Radlkofer. The rapid increase of our knowledge of the African flora is shown by the fact that the number of plants known from this region in 1890 was only about 300.

It is a valuable work that the government is doing to gather together into one series of publications all that is being discovered regarding this hitherto *terra incognita*.— C. R. B.

[2] ENGLER, A.: Monographien afrikanischer Pflanzen-Familien und -Gattungen. III. Combretaceæ — Conbretum, bearbeitet von A. Engler und L. Diels. 4to. pp. iv + 116. *pls. 30. figs. 1.* Leipzig: Wm. Engelmann. *M* 28.

[3] WILDEMAN, EM. DE et DURAND, TH.: Annales du Musée du Congo. Botanique, séries II. Contributions a la flore du Conge. Tome I. Fascicle 1. 4to. pp. iv + 72. Bruxelles: Charles Vande Weghe. July 1899.

Plant diseases.

INFORMATION regarding plant diseases is accumulating so rapidly, and the interest of practical as well as of scientific men is so keen, that frequent issues of books upon one phase or another of the subject may be confidently expected. The latest to reach us is by George Massee,[4] curator in the cryptogamic division of the Royal Kew Herbarium, London. The book is printed and issued in good and convenient form, and is the best manual yet prepared for the British public. Although not so stated, the point of view is mainly the requirements of cultivators in Great Britain; and while much of the work is applicable to the needs of cultivators in North America, yet it is well to remember that the treatment does not always meet the American conditions or state of knowledge, in spite of the fact that the United States is frequently mentioned.

A general description of fungi and of their modes of inducing disease, with an account of fungicides and their application, occupies about fifty pages. The body of the book, about three hundred pages, and the part upon which the usefulness of the work chiefly depends, is devoted to specific plant diseases. The common name is used as the topic heading, supplemented by the name of the fungus in parenthesis. The diseases are grouped according to the relationship of the parasite. Following the body of the work are a hundred pages of technical descriptions of orders, genera, and species of parasitic fungi mentioned in the previous part, designed to provide the cultivator with a means of identifying the fungi he meets with. The usefulness of this portion of the book may be questioned, as it is without keys, or even the names of hosts or the geographical range. It is, indeed, a very dry bit of bookmaking. A good index to parasites and host-plants, unfortunately in two parts, completes the work.

The part of the work dealing with specific diseases is cast in a concise and serviceable form. The disease is clearly described, preventive or curative measures are given, and some important literature is mentioned, in each instance. The large proportion of the facts and citations, under many of the diseases, that are credited to American sources, is a matter of pride to American vegetable pathologists and a guarantee of the usefulness of the work in the hands of the American cultivator. The illustrations are many and excellent.

Very few and only minor errors occur in the book. The old and oft printed statement is made that *Cystopus candidus* does not form oospores in shepherd's-purse, whereas it always does when the fungus invades the flowers. All Gymnosporangia are said to be heteroecious, but the author overlooked the exceptional *G. Bermudianum*.— J. C. A.

[4] MASSEE, GEORGE: A text-book of plant diseases caused by cryptogamic parasites. 12mo. pp. xii + 458. *figs. 92.* London: Duckworth & Co. New York: The Macmillan Company, 1899. $1.60.

Moulds, mildews, and mushrooms.

UNDER the above title Professor Underwood [5] has given us a very interesting little work on fungi and mycetozoa. The volume seems to be a book of today, written especially to aid the American student of this generation and in the hope that it will stimulate and help him in the study of the American fungus flora.

The presentation and background of the work takes the standpoint of taxonomy, but a taxonomy wonderfully free from the dry diagnoses of most systematic descriptions and everywhere combined with interesting accounts of life habits and activities. The orders and families are presented and arranged largely after the treatment followed in "Die natürlichen Pflanzenfamilien." Genera are described for the fleshy fungi, the cup fungi (Pezizales) and certain groups, containing chiefly parasites from the Ascomycetes and Fungi Imperfecti. The groups selected for this more detailed treatment are well chosen as those most likely to satisfy the wants of students who do not have access to special literature, or whose training is insufficient to enable them to find their way through the varied accounts, good, bad and indifferent, which confront beginners at the outset of their studies.

The keys are clear and precise but are likely to demand from the student a considerably greater knowledge of morphology and descriptive mycology than is presented by the text. But, after all, such a background cannot be given by books and comes only through wide acquaintance with the forms in the field and laboratory.

Edible species of fungi receive special treatment, and the book is likely to help many to a clearer idea of the structural marks that are really valuable as specific characters among the fleshy fungi.

The book is greatly to be commended for the historical account of taxonomic work in mycology in our country. There is first a general account, and then, in a chapter on geographical distribution, a brief statement is given of the work done in each of the United States and neighboring countries of Canada, Greenland, Mexico, Central America, and the West Indies. These chapters are likely to prove very interesting to the readers of Professor Underwood's book. Accompanied as they are by a full bibliography, they will be very useful and are sure to give an impetus to further exploration and study. One is constantly impressed with the fact that the whole book is a plea for more work in systematic mycology and more *thorough* work.

Special attention should be called to the admirably chosen and therefore helpful lists of literature following every topic of importance.

As before indicated, the book presupposes some acquaintance on the part of the student with the morphology and life-histories of fungi, and here may

[5] UNDERWOOD, LUCIEN M.: Moulds, mildews, and mushrooms. 12 mo. pp. vi+227; *pl. 10*. New York: Henry Holt & Co. 1899.

possibly be a drawback to a very wide circulation. It will perhaps find its readers among a much older group of students than the writer appears to hope, judging from the popular title and the method of presentation.

As the book pleads so eloquently for more work in systematic mycology, its own success is likely to make more apparent the need of a work presenting an account of the detailed morphology, life histories, and possible relationships of the orders and families. With the advances in so many lines since the work of De Bary, the need of such a text in English cannot be too strongly emphasized.

Professor Underwood's book is a marvel in its compactness, with a wonderfully uniform tone throughout, condensed and yet very clear.—BRADLEY M. DAVIS.

MINOR NOTICES.

M. TH. HUSNOT is indefatigable. Not content with his journal, the *Revue Bryologique*, nor with his *Muscologia Gallica*, *Hepaticologia Gallica*, and *Sphagnologia Europæa* with their 142 plates, not to mention many smaller works, nor with his *Musci Galliæ*, *Hepaticæ Galliæ*, and other exsiccatæ, with their 1300 numbers, he now puts before the botanical public a quarto fascicle of almost 100 pages and 33 plates, describing and figuring the grasses, wild and cultivated, of France, Belgium, Great Britain, and Switzerland.[6] More than this, M. Husnot is his own draughtsman, lithographer, and publisher.

The quarto form has been adopted partly for economy and partly for the convenience of the large plates, allowing a considerable number of allied species to be drawn side by side. The letter press is double columned and compact. In substance the text is such as one finds in a manual rather than a monograph. The plates are fairly accurate, their most conspicuous defects being in some of the figures of habit. Details of the flowers are shown and keys to genera and species are given. Altogether, but for its unwieldy form, the author has produced a useful work for the botanists and cultivators of western Europe.—C. R. B.

VOLUME XX of the *Transactions* of the American Microscopical Society contains three papers of interest to bacteriologists and an elaborate study of the primary meristem of thirteen species of Caryophyllales, by Dr. F. E. Clements of the University of Nebraska. The bacteriological papers are "The persistence of bacteria in the milk ducts of the cow's udder" by A. R. Ward; "Experiments in feeding some insects with cultures of comma or cholera bacilli" by R. L. Maddox; and "Questions in regard to the diphtheria bacillus" by M. A. Veeder. An abstract of a portion of Dr. Clements'

[6] HUSNOT, TH.: Graminées: descriptions, figures et usages des graminées spontanées et cultivées de France, Belgique, Iles Britanniques, Suisse. 4to. pp. viii + 92. *pls.* 33. **Cahan, par Athis (Orne): Th. Husnot. 1896–1899. 25 francs.**

paper was published in this journal some time ago.[7] Dr. Clements has investigated the transition region from root to stem, the origin and development of radicels, and the apical growth of the stem. He describes three types in the transition region (BOT. GAZ., *l. c.*) and finds no anatomical characters of value for taxonomic purposes. Van Tieghem's conclusions that the radicels arise always and entirely from the pericycle and that there is but one type of radicellar formation in dicots are confirmed. As to apical growth, two or three initial cells are found in all the group, and Douliot's opinion that apices with two initials are more primitive while three belong to higher forms is supported. The volume is well gotten up and is a credit to the society.—C. R. B.

ONE OF THE most thorough pieces of bryological work which has yet appeared in this country is the monograph on the Hepaticæ of California which was issued in August last by Dr. Marshall A. Howe, of Columbia University.[8] Eighty-six species are fully described, and a number of them figured on well drawn plates. Full synonymy and remarks regarding nomenclature, differential characters, distribution, etc., provide the necessary critical apparatus for students of the group.

Dr. Howe abandons, for the first time in taxonomic work, the coordination of the Anthocerotales with the Marchantiales and Jungermanniales, and raises them to the rank of a class of the Bryophyta coordinate with the Hepaticæ and Musci. While perhaps not entitled to speak on this point, we incline to a less radical step, such as dividing the Hepaticæ into two sub-classes, Eu-hepaticæ and Anthocerotes.

The descriptions are long, seldom less than half a page, and do not indicate the diagnostic characters; a lack which is partly supplied by the keys to species, when more than one occurs in the region, and partly by supplementary remarks. The modern morphological terms occasionally replace the conventional ones, but there is, unfortunately no consistency in this usage, sporophyte and sporogonium and capsule, receptacle and gametophore, thallus and plant being used without apparent system. The plates are quite unlike the ordinary taxonomic ones, giving many morphological details, as do the descriptions. The monograph therefore will be welcomed by both bryologists and morphologists.—C. R. B.

THOSE who have used Professor Macbride's monograph on the Myxomycetes of eastern Iowa will welcome the more extensive account furnished by the present volume which gives descriptions of all species of Myxomycetes hitherto described from North America including Central America.[9] An introductory

[7] BOT. GAZ. **24**: 182. 1897.

[8] HOWE, M. A.: The Hepaticæ and Anthocerotes of California. Memoirs of the Torrey Botanical Club **7**: 1–208. *pl. 88–122.* 5 Aug. 1899.

[9] MACBRIDE, THOS. H.: The North American slime molds. 8vo. pp. xvii + 269; *pl. 18.* New York: The Macmillan Company. 1899. $2.25.

chapter gives a description of the habit, habitat and life history of the group, and a discussion of the nomenclature. Directions are given for collecting and preserving specimens.

The æthalioid forms are regarded as the most primitive, while the isolated sporangium with its capillitium is the highest expression of myxomycetous fructification, reached by successive differentiations from the simple plasmodium. The artificial keys follow this sequence. As in the previous monograph, the keys are clear and the descriptions are accompanied by a full synonymy. The plates are well drawn and should readily enable the student to recognize in actual preparations the structures which the figures are intended to illustrate.—CHARLES J. CHAMBERLAIN.

IN examining garden soils near Cambridge University (England) Dr. W. C. Sturgis isolated and studied a large soil bacillus of the type of De Bary's *B. Megatherium*. Of its peculiar life history and morphology he gives an extended account in Phil. Trans. Roy. Soc. London B. **191**: 147–169. *pl. 14–16.* 1899.

LIEFERUNGEN 4 and 5, completing the second edition of the *Flora* of the northeast German Lowlands, have been published.[10]

Nothing need be added to the notice of the earlier parts.[11] The general form and the details of typography are admirable for a field manual. It was announced that the price for the complete work would be raised above the subscription price of *M* 16.50, already high.—C. R. B.

NOTES FOR STUDENTS.

IN THE *Transactions* of the Royal Society of London (B. **190**: 531–621) Mr. Francis Darwin has published the results of interesting investigations on the behavior of stomata. He departs somewhat from the methods of previous investigators, which he does not consider very reliable, and uses the hygroscope method suggested by him some years ago. He has improved upon the stipa hygroscope, using now hygroscopes made of horn shavings and strips of the dried epidermis of *Yucca aloifolia*, so attached to a bit of cardboard bearing graduations that the degree of curvature induced by the moisture from open stomata can be read. The horn hygroscope is quite reliable and has the advantage of showing in a few seconds whether the stomata are open or closed, while the Yucca hygroscope can be used to study accumulating moisture. His results frequently differ from those of previous investigators.

[10] ASCHERSON, P., and GRAEBNER, P.: Flora des Nordostdeutschen Flachlandes (ausser Ostpreussen). Zweite Auflage. Lieferungen 4. 5. 12mo. pp. 481–875. Berlin: Gebrüder Borntraeger 1898. *M* 7.80.

[11] BOT. GAZ. **26**: 363. 1898.

The more important results which he established are as follows: He finds an almost universal closing of the stomata of terrestrial plants during withering, though in almost all cases complete closure is delaved, and after several hours the stomatal transpiration still greatly exceeds the cuticular. The closure is usually preceded by a temporary opening, due to the diminished epidermal pressure on the guard cells. This can be produced more readily in the morning before the stomata naturally open, but not at night after they are closed, and is especially noticeable in laticiferous plants. In many aquatics and marsh plants there is at least a partial closure upon withering, but as a class they do not close to the degree observed in land plants. In many cases where there is no apparent movement at first, closure sets in several hours after withering, and the author asserts his opinion that in no case are the stomata entirely immobile. That closure is correlated with diminished water supply is shown by the invariable closure when the stem is compressed in a vise, and opening when released. Dry air causes closure though the leaves show no signs of flaccidity, and in very dry air the closure is preceded by a prolonged "preliminary opening." The stomata are opened by weak electric currents, but stronger shocks close them. In chloroform and ether vapor they close slowly and then open again, and in CO_2 they slowly close. In bright sunshine they are more widely open than in diffused light, and they close on dark stormy days even in summer. Artificial darkness usually produces closure, and opening occurs when again illuminated, but the time required in each case depends upon the time of day, the normal "daily period" being quite marked. Of the large number of unspecialized terrestrial species tested, only a small percentage do not close their stomata at night. Among nyctitropic plants, whether terrestrial or aquatic, the great majority do not close the stomata at night, and especially if the temperature be fairly high. Even among unspecialized terrestrials, Darwin considers that the closure is not so complete as to prevent transpiration, though it greatly diminishes it. He discusses at some length the ecology of nocturnal closure, but does not seem to think that we know enough about its effects to justify definite conclusions, though he considers the economy of water and of heat to be important factors. A strong tendency toward a daily periodicity is apparent, for much less light opens the stomata in the morning than in the afternoon; conversely, it takes much longer exposure to darkness to close them in the morning than in the afternoon. Dry heat tends to open the stomata; and of the visible spectrum the red rays are the most effective. The effect of prolonged darkness is to reopen the stomata.

The question of the mechanism of the stoma is discussed at some length, and the author seems to think that it is in about the same condition in which von Mohl left it in 1856. As to the immediate cause of the movement, he combines the views of Leitgeb and Schwendener, and holds that it

depends upon the correlation between the pressure of epidermal and guard cells. The phenomenon he considers as one of irritability, the same as nyctitropic or other irritable movements. An excellent bibliography is appended. —W. B. McCallum.

Professor Pfeffer, in a lecture upon reproduction and the significance of amitosis,[12] calls attention to the fact that the comparative rarity of the amitotic division of the nucleus, together with the enormous attention paid to karyokinetic figures, has led to the belief that cells which show amitosis have lost their reproductive power, and that direct nuclear division presages the death of the cell, a view which is upheld by Strasburger, Ziegler, von Rath, and many other prominent animal and plant cytologists. That this view is erroneous is proved by the behavior of Spirogyra under certain conditions of culture. The cells of this plant continued to grow and divide amitotically for periods of twelve hours or more, the protoplasmic structures produced being in all respects similar to those coming from mitotic divisions, and when the plants were removed to a normal medium the customary methods of cell-multiplication were resumed without variation. The same treatment induced amitotic division in Closterium, and also in the stamen hairs of Tradescantia, but failed to do so in Phaseolus and Lupinus.

Mitosis and amitosis were observed in neighboring cells in callus formations, and the total results from all the material examined show that amitosis may occur in young rapidly growing embryonic tissue as well as in older cells. The occurrence of either method of nuclear division is under control of the regulatory mechanism of the cell. Both are performed as specific reactions to environmental conditions, and intermediate stages of division may be sought for during the alteration of these external conditions. It is not improbable that even such highly specialized structures as egg cells may divide at certain times by amitosis.

It follows that the nuclear figures are not vehicles of heredity in the sense in which they have been so widely considered, a conclusion which has already forced itself upon the workers who have gone most deeply into the subject. Not only must less hereditary value be conceded to the chromosomes, but it must be admitted that the nucleus is not the sole bearer of the qualities of the organism or cell.—D. T. MacDougal.

Botanists probably do not fully appreciate the value of the *Experiment Station Record*, issued by the Department of Agriculture, as an index to current literature. In the tenth volume, just completed, over 2000 articles have been abstracted, of which more than 1200 were foreign. Of these abstracts 127 are classified under botany; 27 under fermentation and bacteriology; 34

[12] Abhandl. d. Math.-Phys. Classe d. Konigl. Sachs. Ges. d. Wiss. zu Leipzig. Sitzung von 3 Juli, 1899.

under forestry; 37 under seeds and weeds; and 180 under diseases of plants; making over 400 with a distinct botanical bearing. Besides these there are abstracts under chemistry, soils, field crops, and horticulture which are often of direct interest to botanists.

INTERESTING INFORMATION regarding rubber of various kinds, its origin, collection, preparation, etc., will be found in recent *Circulars* of the Royal Botanic Gardens of Ceylon, and the *Bulletins* of the Royal Gardens at Kew. Many insects and fungus enemies, some of local origin, some introduced from Assam and elsewhere, are now attacking tea in many parts of Ceylon. The gray blight, a leaf disease due to *Pestalozzia Guepini*, and brown blight, due to *Colletotrichum Camelliæ*, are both now to be found in most districts.—C. R. B.

MR. ATSUSHI YASUDA has in hand work on the influence of inorganic salts upon the conidia formation of *Asperigillus niger*.[13] He finds that increasing concentration of the solutions of K, Na, NH_4, and Mg salts retards the formation of conidia, reduces the size of the fruits, shortens the conidiophores, and promotes the blackening of the conidia. When very concentrated the formation of conidia is suppressed.—C. R. B.

DR. A. J. GROUT suggests[14] that to devise a truly natural classification of the pleurocarpous mosses much more consideration must be given to gametophytic characters than hitherto, since all arrangements based mainly on sporophytic characters produce juxtapositions of unrelated species, of which he cites abundant illustrations. He is not yet ready, however, to propose a new grouping.—C. R. B.

MR. GEO. MASSEE has a revision of the twenty-six species of Tiletia in the *Bulletin of Miscellaneous Information*, at Kew Gardens, nos. 153, 154. The United States is credited with nine species, ranking next to the continent of Europe with thirteen species.—C. R. B.

A MONOGRAPH of the Danish blue-green algæ is published by John Schmidt in the *Botanisk Tidsskrift* **22**: 283–418. 1899. It is illustrated by thirty-eight figures.—C. R. B.

[13] Tokyo Bot. Mag. **13**: 85. 1899.

[14] Revue Bryologique **26**: 72–77. 1899.

NEWS.

WITH THE December number 1899, completing the fifteenth volume, *Natural Science* announces its suspension on account of inadequate financial support.

MISS FANNY E. LANGDON, formerly instructor in botany in the University of Michigan, died at Ann Arbor, October 21, 1899, after an operation for appendicitis.

FROM *Science* we learn that Dr. H. M. Richards, instructor in botany in Barnard College, has been compelled by ill health to relinquish his courses and has sailed for Europe.

DR. B. L. ROBINSON, the curator of the Gray Herbarium, has been appointed to a new chair established in Harvard University, the Asa Gray professorship of systematic botany.

ABOUT 200 volumes from the library of the botanist David Hosack have been presented to the New York Botanical Garden. They are in excellent condition and some of them are very rare.

DR. C. V. PIPER, of Washington Agricultural College, has been granted a year's leave of absence, which he is spending in work upon the Washington flora at the Gray Herbarium of Harvard University.

DR. W. G. FARLOW, of Harvard University, and Miss Lilian Horsford, of Cambridge, Mass., were married on January 10. Dr. Farlow will receive the congratulations and best wishes of a host of botanical friends.

MESSRS. HENRY HOLT & CO., announce for immediate publication Atkinson's *Lessons in Botany* and Barnes' *Outlines of Plant Life*. Both books are simplified and abbreviated editions of earlier books by the same authors.

PROFESSOR J. W. TOUMEY, of the University of Arizona, will spend half of the present year at Washington on the staff of the Division of Forestry. During his absence his work will be carried on by Dr. A. A. Tyler, who has been appointed assistant botanist.

PROFESSOR L. F. HENDERSON, of the University of Idaho, has been granted leave of absence from January 1900 till the opening of the next college year. He will study the greater part of the time at the Gray Herbarium of Harvard University, and at Cornell University.

THE GENERAL herbarium of the late Dr. Böckeler, of Varel, will be sold. It contains about 12,000 species and is very complete for the European flora. Several exotic sets are also included, and some families from the herbarium of Kurt Sprengel. Further details may be obtained by addressing H. Graf zu Solms-Laubach, Strassburg, the editor of *Botanische Zeitung*.

A FULL-LENGTH oil portrait of Linnaeus was presented to the Philadelphia Academy of Natural Sciences at the meeting on Tuesday, December 26, by Mr. Charles E. Smith, a veteran botanist of Philadelphia. The portrait is a copy of the original painting in the possession of Baron Verschner of Holland. It was made for Mr. Smith by Boudewynse with the permission of the owner. It represents Linnaeus in early manhood, in the dress he wore when making a journey to Lapland. Engravings of this portrait are not rare.

THE FIRST number of the new *Bulletin de l'Institut Botanique de Buitenzorg* contains an account of the present condition of the institute, its staff, publications, garden and laboratory facilities; of the climate; of the opportunities it offers to visiting naturalists, with suggestions and information of special value to those who contemplate going thither. Since 1885, seventy-five naturalists have visited the garden, of whom twenty-two were from Holland and nineteen from Germany; Austria coming next with nine, while only one American, Mr. Fairchild, has been there for study. Plans of the gardens and buildings are also shown.

THE ANNOUNCEMENT of the department of botany for the thirteenth season of the Woods Hole Marine Biological Laboratory has been issued unusually early. The session is to begin Thursday July 5 and close on Thursday August 16. The staff consists of Dr. Bradley M. Davis, in charge, Mr. Geo. T. Moore, and Dr. Rodney H. True; with Mrs. Rhoda A. Esten as curator of the herbarium and Miss Lillian G. MacRae as collector. Courses (lectures and laboratory work) will be offered in cryptogamic botany, physiology, and cytology. Besides this, there will be the usual course of general lectures of which the details cannot yet be announced. A course in "nature study" will be offered this year for the first time. The announcement may be obtained by application to Dr. B. M. Davis, the University of Chicago.

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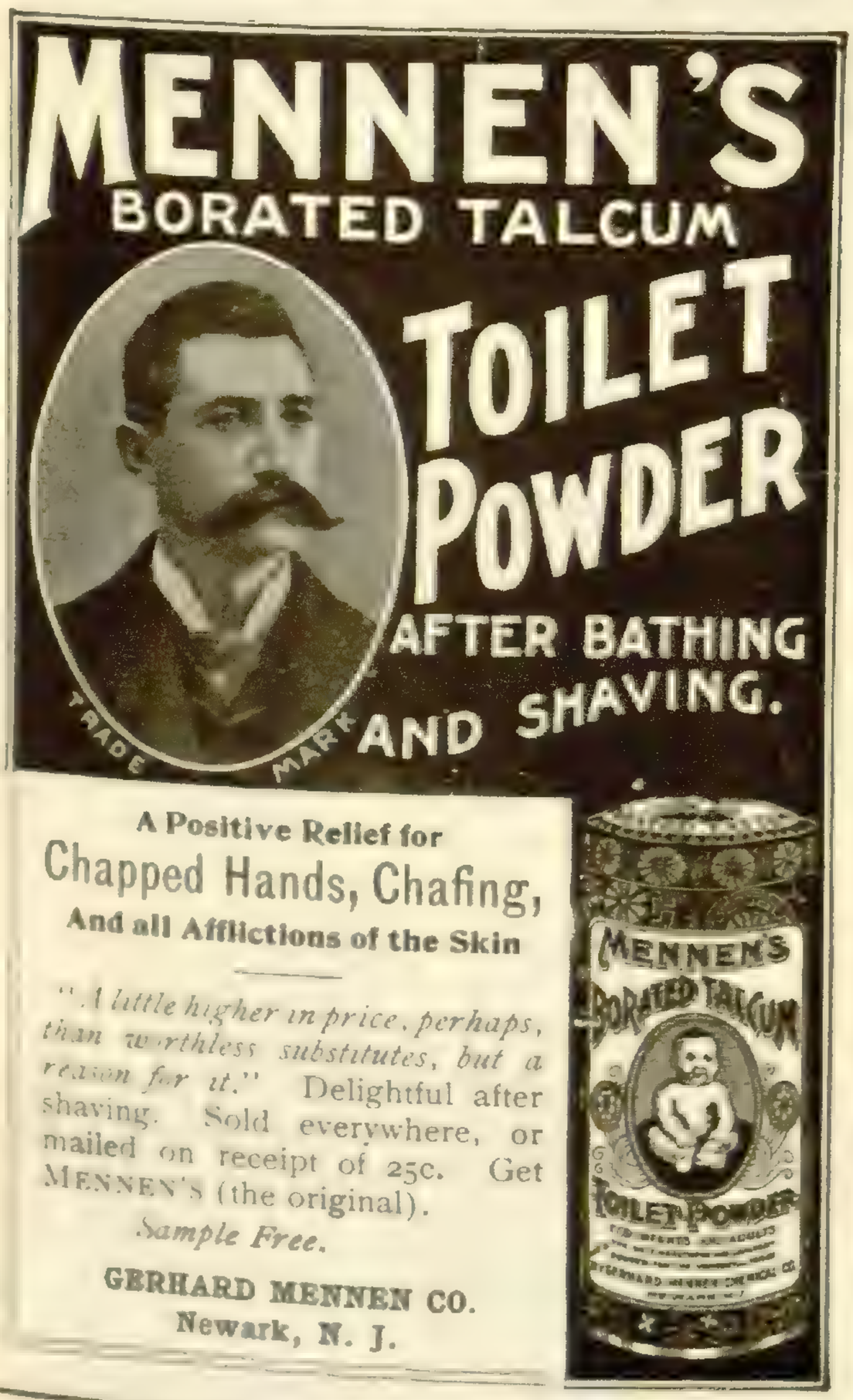
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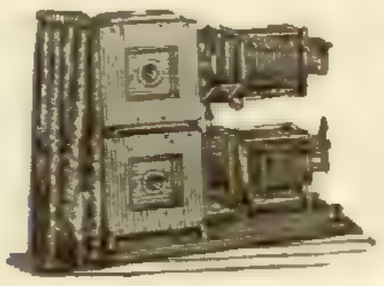

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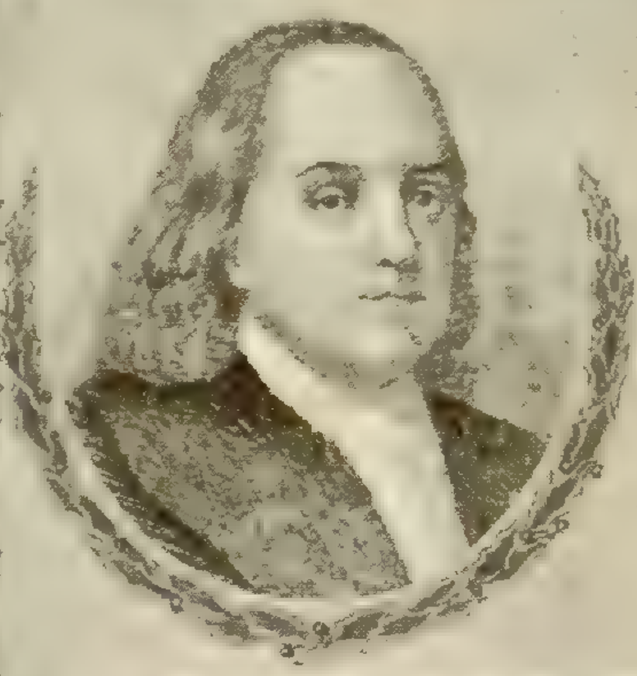

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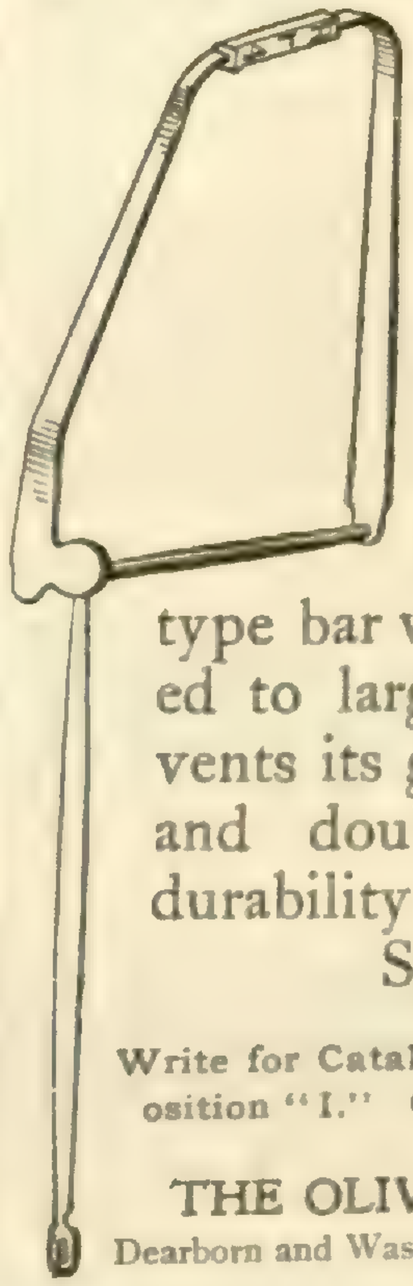

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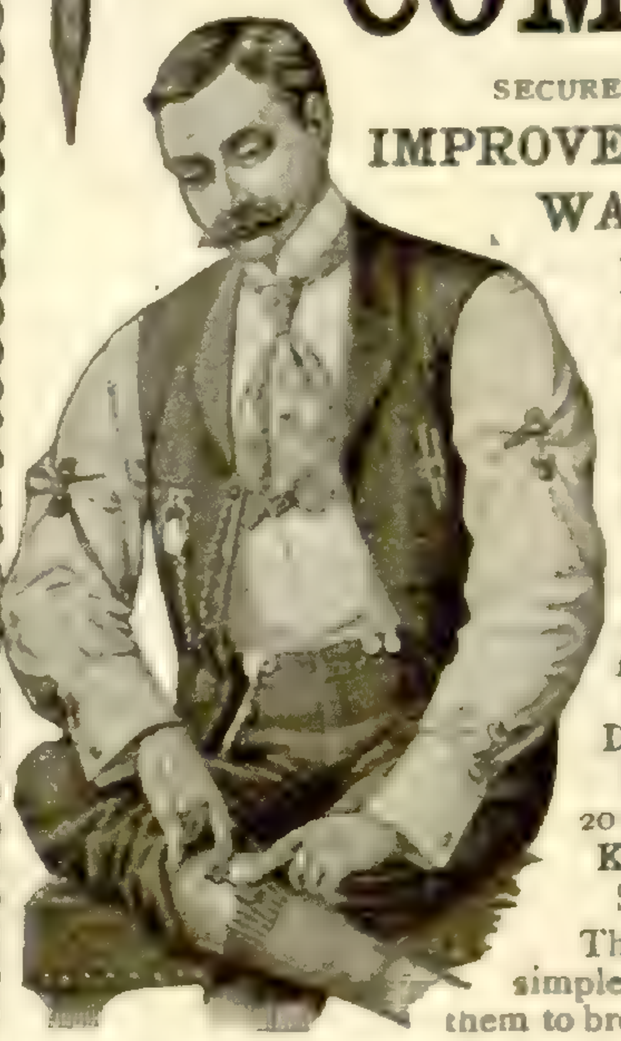

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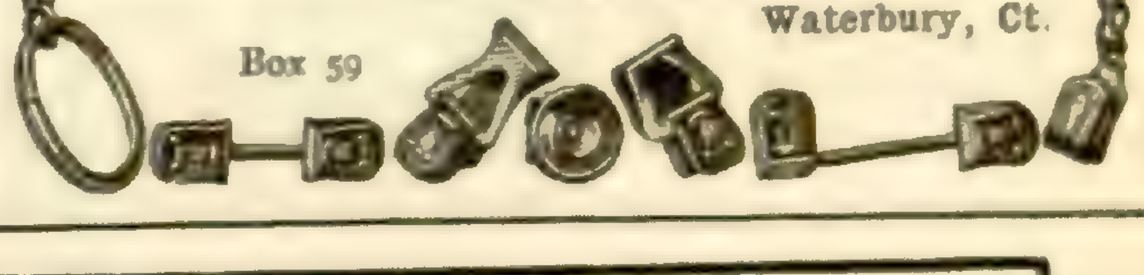

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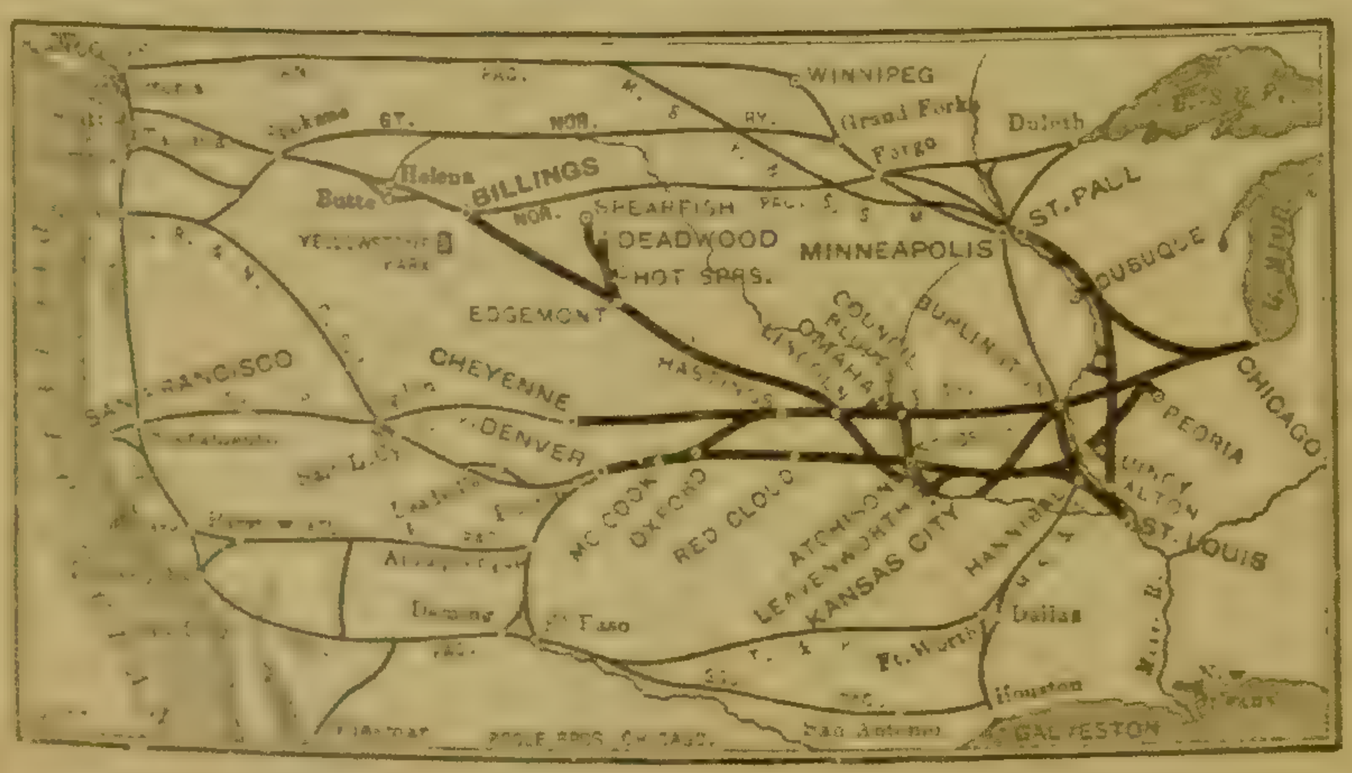

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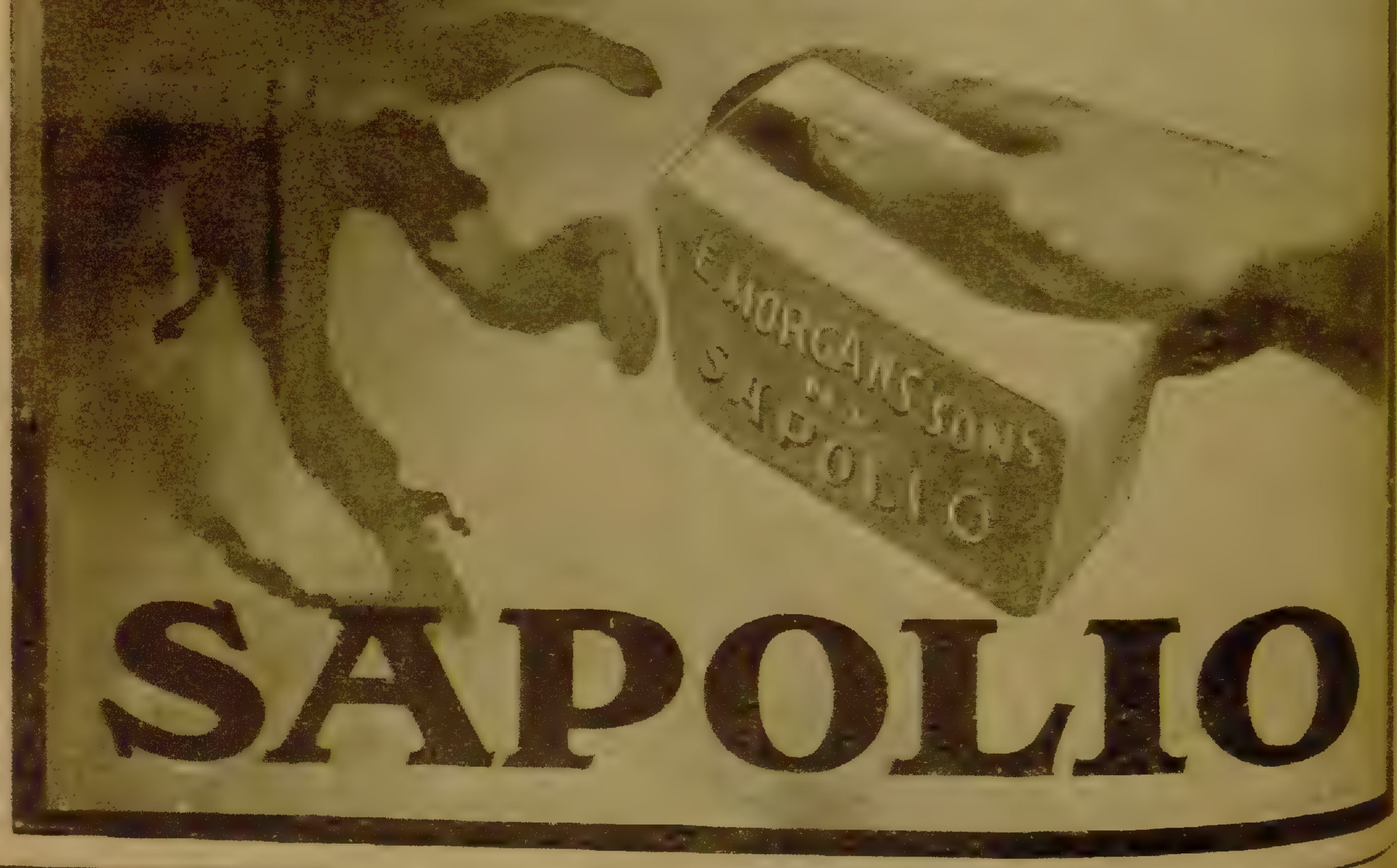

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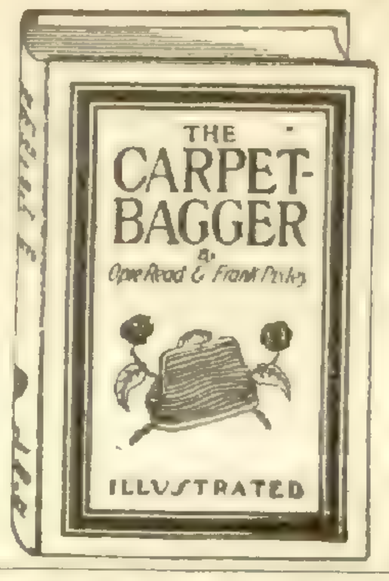

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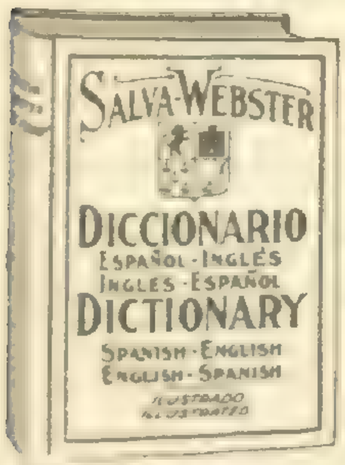

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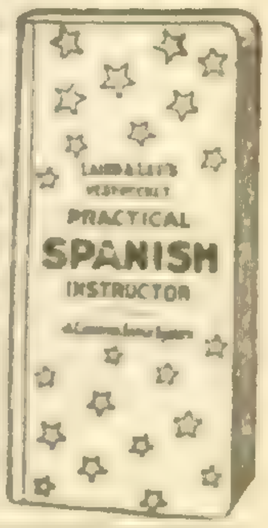

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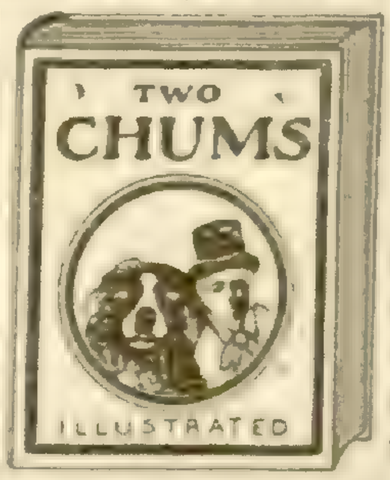

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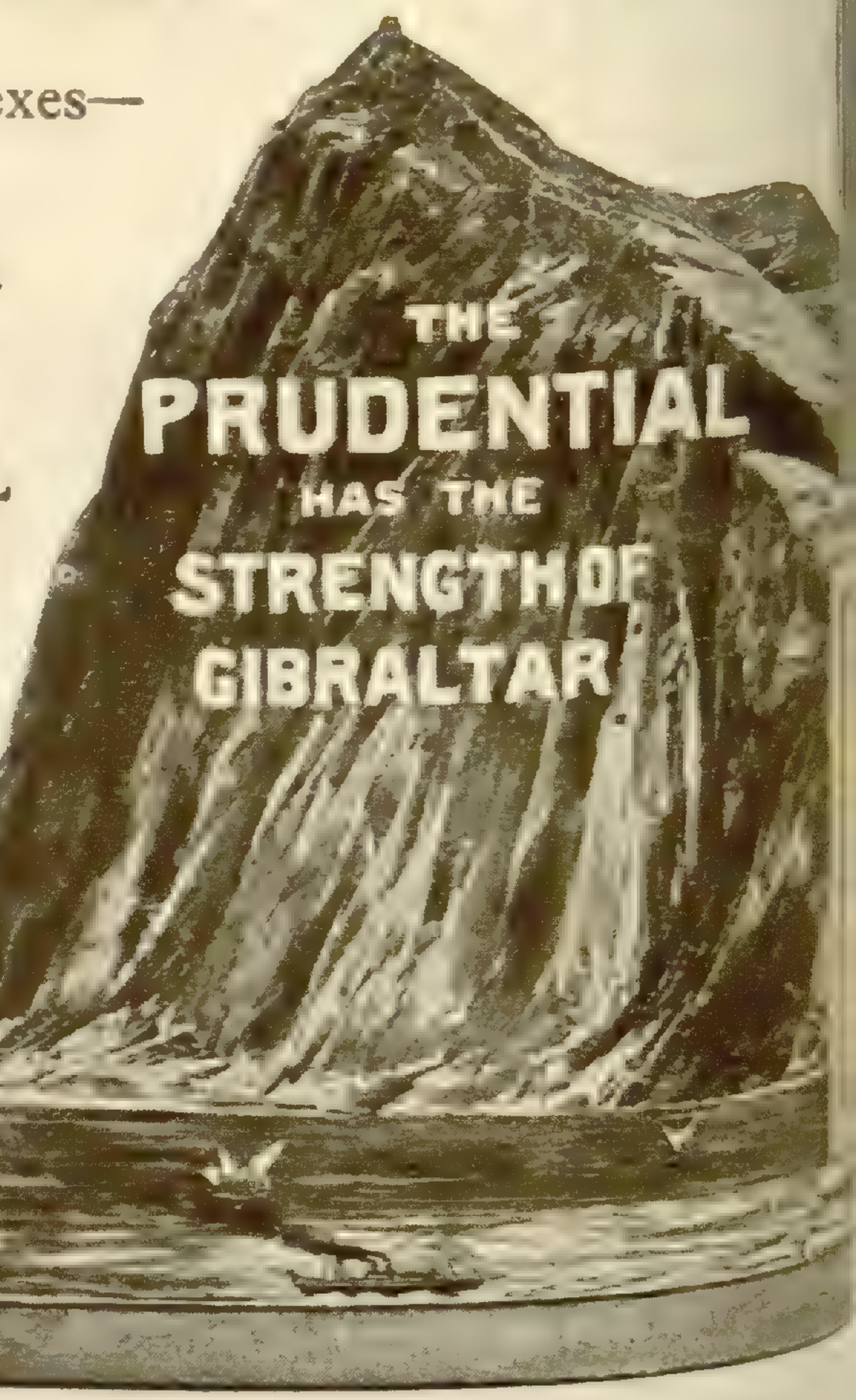

VOLUME XXIX NUMBER 2

BOTANICAL GAZETTE

FEBRUARY 1900

STUDIES IN THE DEVELOPMENT OF THE POLLEN GRAIN IN SYMPLOCARPUS FOETIDUS AND PEL-

Plates I and II will be issued with the March number.

either plant, but in Peltandra there were found stages showing the divisions in the archesporial cells. These divisions are of the normal vegetative type; the number of chromosomes present, moreover, is that characteristic of the sporophyte.

THE RESTING ARCHESPORIAL CELL AND ITS NUCLEUS.

In Symplocarpus the cells of the definitive archesporium pass the late fall and early winter months in the resting condition.

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STUDIES IN THE DEVELOPMENT OF THE POLLEN GRAIN IN SYMPLOCARPUS FŒTIDUS AND PELTANDRA UNDULATA.

B. M. DUGGAR.

(WITH PLATES I AND II)

DETAILS of the nuclear and cell division in the development of the pollen grain in these plants were first studied in *Symplocarpus fœtidus*, an abundance of favorable material having been secured and satisfactorily preserved during the winter of 1897–8. When it afterwards seemed well to study another plant in the same order, Professor Atkinson kindly put at my disposal material of *Peltandra undulata* which he had collected two years earlier. The latter material was also well fixed and preserved; but since it gave fewer developmental phases, Peltandra has been used largely by way of comparison with Symplocarpus. In general, these two plants agree in important phases of the cell activities, but there is considerable variation in some details.

The origin of the primitive archesporium was not studied in either plant, but in Peltandra there were found stages showing the divisions in the archesporial cells. These divisions are of the normal vegetative type; the number of chromosomes present, moreover, is that characteristic of the sporophyte.

THE RESTING ARCHESPORIAL CELL AND ITS NUCLEUS.

In Symplocarpus the cells of the definitive archesporium pass the late fall and early winter months in the resting condition.

Except in the size of the cells, no change was noticeable from early November to about January 1.

In the resting stage the cytoplasm is closely netted in the vicinity of the nuclear membrane, but there is no indication of a felt-like mass of kinoplasm. The nuclear membrane is more clearly defined than during the prophase of division. The nucleolus is more or less spherical, usually with at least one slight projection in view, the latter seeming to unite the nucleolus with the general reticulum. With gentian violet in the Flemming combination, the nucleolus stains a homogeneous purple; but with hæmatoxylin minute vacuolate appearances are often noted. Two or three smaller bodies resembling nucleoli may be present, and they are usually attached to distant parts of the reticulum.

At this time the reticulum is very slightly chromatic. It is loosely netted, with an indication of smaller knots at the anastomoses, and numerous small chromatin granules are scattered on the thread. In the reticulum stage, in fact, the nucleolus is the only nuclear structure which takes the chromatin stain freely, and very little indication of the safranin is retained after the use of the gentian violet.

SYNAPSIS.

Changes in the resting nucleus leading to the first evidence of a spirem and to the condition of synapsis have not been found abundantly. The threads of the reticulum become somewhat thicker, and the scattered granules upon it stain more deeply. Invariably these changes seem to precede that contracted condition of the linin network, or early spirem, well known as synapsis. Synapsis has been found abundantly at a definite period in the development of the pollen grains in these plants. In Symplocarpus there was no indication of this condition in material collected before the latter part of December; but for more than a month afterward it was often found, along with other stages, either later or earlier.

In both of these plants during the condition of synapsis the nucleolus becomes slightly wasted in appearance. The linin

framework contracts, at first irregularly. Finally it becomes closely pressed together, or "balled up," so that individual linin elements cannot well be distinguished, except where there are a few loose ends apparently serving for attachment to the nuclear membrane (*fig. 1*). The nucleolus is usually embraced in this contracted mass on one side, so that it protrudes prominently. Even in this condition, one or more slight projections on the nucleolus may sometimes be seen on the side near the contracted mass. The interwoven linin substance takes a diffuse stain. In the general mass there are also globules of a deeper staining substance. The nucleus does not become spread out against the wall, as described in some cases;[1] but it is usually situated on the side of the contracted mass distant from the wall. The contracted mass is either in contact with the nuclear membrane, or connected with the latter by linin threads.

During synapsis the cytoplasm becomes more loosely netted; and in Symplocarpus there is often an assemblage of kinoplasmic elements in that part of the cell which contains the greatest amount of protoplasm. These fibers are hardly so arranged as to be termed a cytoaster; and their general position may be either radial or oblique to the wall. A considerable number of large, deeply-staining granules are distributed in the cytoplasm. Another change which seems to be dependent upon synapsis is noted in the smaller nucleolar-like bodies of the nucleus. As separate bodies, any of these which may have existed in the resting condition disappear during synapsis, or they become closely adherent to the nucleolus and indistinguishable from the budded appearance of the nucleolus in the spirem, as mentioned later.

Synapsis has been found at a definite stage in the sporogenesis of many plants.[2] The marked differences noted in the stages

[1] SARGANT: The formation of the sexual nuclei in *Lilium Martagon*. I. Oogenesis. Ann. Bot. 1: 457. 1896.

[2] Cf. *a*) FARMER: On spore formation and nuclear division in the Hepaticæ. Ann. Bot. 9: 473, 481, 490. 1895.

b) STRASBURGER: Theilungsvorgang des Zellkerne, *figs. 3, 66.*

c) CALKINS: Chromatin-reduction and tetrad-formation in pteridophytes. Bull. Torr. Bot. Club 24: *fig. 3*. 1897.

d) SARGANT: *l. c.*, also, II, Spermatogenesis. Ann. Bot. 11: 187. 1897.

before and after this condition indicate that in some obscure way it must have an effect in the distribution of chromatin to the spirem ribbon. The changes evident on the return of the chromatin substance from synapsis are gradual but well marked. All phases of the return from this condition and leading to the spirem stage may be traced in a single anther.

It has been suggested by some that during the early prophase of division the cytoplasm is more difficult to fix, and from this difficulty may result the contraction termed synapsis. There is, however, little evidence for assuming that the cytoplasm is then so difficult to fix, nor is this condition a constant attendant of improper fixing during early prophase stages. The effect of diffusion currents, moreover, could not well produce such effects as found in Symplocarpus, since diffusion currents sufficiently strong to wrap the thread into a chromatic ball would hardly leave the nucleolus attached in the characteristic manner mentioned.

THE SPIREM STAGE AND SEGMENTATION.

On freeing itself from the contracted condition by a gradual loosening of the coils, the spirem skein in Symplocarpus takes the gentian readily, and it is easily traced as one or few coils with no anastomoses. The wide looping of the coil is more evident at this period than at any other. The thread is then made up of numerous adjacent disks of chromatin substance almost homogeneous with the linin connections. The chromatin disks become more distinct, and the ribbon spaces more noticeable; hence a somewhat nodulate appearance is presented, as in *fig. 2*. No evidence of a longitudinal splitting of the ribbon can be found at this time.

During the initiation of the spirem stage the nucleolus has a distinctly budded form, sometimes consisting of a single large body and of one or two smaller ones closely united, or two of nearly equal size. It is often very clear that the spirem thread is connected with these nuclear parts.

Following that stage in Symplocarpus where the spirem thread is uniform, there occurs a more abrupt bending and twisting of

the ribbon. Coincident with this, there is a thickening and a contraction in these looped regions. In some cases this thickening seems to be uniform; but generally there are very definite chromatin masses. Gradually these chromatin masses increase in size, and most of the chromatin disappears from the connecting regions.

The above changes lead to a condition very striking in appearance. At many places where thickening has occurred, there are several, usually about four, distinct chromatin aggregations (*fig. 3*). These are usually arranged in such a position as to suggest a division in two directions; hence a tetrad in the sense of the Freiburg school of zoologists. In many other instances there are distinct links open at one end, although the chromatin is in masses in these links. X and Y forms are much less common (*fig. 4*). A study of the changes leading to these conditions, however, seems to exclude the probability of tetrad-formation. Moreover, when viewed in the plane of the link there is indication of a longitudinal division in the linin connections between the chromatin masses, but never very marked. It is probable that the ribbon bends upon itself abruptly in the regions of the thickened chromatin masses to make the link forms, and that diverging forms are to be ascribed to a partial separation and reunion at the bend. If we accept this interpretation each chromatin group represents two chromosomes attached end to end and bent upon each other, with only a local indication of longitudinal fission, giving ultimately an effect such as others have described for Lilium; also for Helleborus, Podophyllum, Iris, and other plants. As these loops or chromatin groups increase in size, the indication of chromatin granules in the connecting linin diminishes. During early segmentation the prominence of these linin connections seems paralleled in certain Hepaticae studied by Farmer.[3]

During the aggregation of the chromatin into definite groups, important changes occur in the nucleolus. From the time when the large nucleolus is in close connection with one or more

[3] *Loc. cit.*, p. 8, *figs. 5, 6, 41*.

smaller ones, the group gradually becomes fused, or the smaller bud-like processes disappear. The nucleolus is then drawn out in one or more directions so as to appear elliptical or triangular, or even rectilinear (*figs. 3, 4, 5*). It is, however, generally elliptical. Whatever may be the shape during this formative period of the chromosomes, the nucleolus is connected with certain linin threads, and it is evidently drawn out toward them. Often when the nucleolus appears circular in outline, by proper focusing certain attachments above or below may be seen. The fusiform and closely budded condition of the nucleolus was noted in living material, and I anticipated finding the *Sickelstadium* of Zimmermann.[4]

The chromosomes increase rapidly in size with the gradual disappearance of the chromatin from the linin connections. The incomplete union of the two segments in the process of bending back is often evident until the disappearance of the nuclear membrane, at which time the chromosomes tend to collect at the periphery of the nucleus. I have observed no protrusion of bundles of kinoplasm into the nuclear hollow before the separation of the fibers forming the nuclear membrane.

The spirem stage and the formation of the chromosomes are somewhat different in Peltandra from that which obtains in Symplocarpus, but I have fewer stages from which to draw conclusions. At no time can the spirem ribbon be distinguished as a loose coil. It twists and bends upon itself so freely as to suggest anastomoses (*fig. 15*). There are not such definite granules upon the ribbon, and the staining is much more homogeneous. Nothing which could be interpreted as a general longitudinal division of the ribbon was observed. On the other hand, it gradually becomes thicker where there seem to be anastomoses, and with further growth the whole extent of the skein is much shortened, and the chromatin thickenings are connected by slender threads, as in *fig. 16*. The nucleolus is often fusiform; but it never presents such exaggerated forms as in Symplocarpus. Each

[4] ZIMMERMANN: Über das Verhalten der Nukleolen während der Karyokinese. Beiträge z. Morph. u. Phys. d. Pflanzen.

nuclear segment bends upon itself, as in *fig. 17*, and with further growth the normal size is attained. The cytoplasm in Peltandra is very loosely netted, and in the vicinity of the nuclear membrane a marked radial arrangement of kinoplasmic fibers is evident during the late stages of chromosome formation, as has been abundantly described and figured (*figs. 17, 18*).

THE FIRST DIVISION.

On the disappearance of the nuclear membrane in Symplocarpus the kinoplasmic fibers entering the nuclear hollow are quickly oriented as a multipolar spindle with rather indefinite apices. The chromosomes are irregularly disposed on these fibers. The next most abundant stage is a multipolar spindle of very few poles, as in *fig. 6*. Finally a bipolar spindle is formed, the apices of which do not end in a very definite point (*fig. 8*).

When arranged upon the nuclear plate, it is difficult to interpret the exact form of the chromosomes in Symplocarpus, as they are so short and thick that fission lines and lines of union are almost indistinguishable. Looking down upon the chromosomes in an axial view, they seem to be somewhat quadrangular. A side view of a single segment shows the line along which separation will take place; and a polar view, *fig. 7a*, seems to indicate that the knee representing the original bend must be directed toward the center. It would be difficult at this stage to determine which plane represents the longitudinal fission and which the line of union of the doubled segment. The fission in a median plane is more distinct, and the external tips separate farther in this plane, as at *a*, *fig. 7*. Usually this is so evident, even before there is any separation of the daughter segments, as to make credible the view that they are so disposed as to separate qualitatively at the first division.

In Peltandra there is a less definite multipolar spindle than in Symplocarpus, although in the former the general form of a multipolar spindle is evident (*fig. 19*). With the completion of the bipolar form, the chromosomes are both centrally and peripherally disposed. The complete spindle is drawn together loosely

at the poles. There is a tendency for the polar cytoplasm to arrange itself radially.

The short chromosomes of Peltandra, which are sometimes of a short Y form are closely arranged on the nuclear plate, evidently with the knee inward. In the vicinity of the knee are attached the spindle fibers. If there is then any noticeable separation, indicating double V or Y forms, this separation is in the equatorial plane, thus giving the normal nuclear plate arrangement with longitudinal fission. The form of the chromosomes during the separation into the daughter segments (*fig. 20*) supports this view. The form of the short daughter segments soon after separation is somewhat oblong heart shaped, since the angles of the V and Y forms seem to shorten and to fuse.

If, however, my interpretation of the condition of things in Symplocarpus is correct, the separation at the nuclear plate stage of the first division brings about a transverse division. Then, as suggested to me by Professor Atkinson, the closely following second division would provide for the separation of the segments marked out by the first division. Korschelt[5] states that in *Ophryotrocha puerilis* reduction is effected during the first division.

There are about twenty-two chromosomes, and when they are arranged on the nuclear plate, a polar view may give the idea that they are variously fused. This appearance, however, is only due to the fact that the staining does not make evident the lines of contact, and a slightly oblique view aids the deception.

Radiations as of extra spindle fibers, which in some way are set free during the splitting of the chromosomes, veil the central spindle, and reach out almost to the periphery of the cell in the middle diameter of the spindle.

Cytoplasmic granules staining deeply are quite numerous in peripheral regions, and in Peltandra they are exceptionally large. In all stages of the developing and complete spindle, special attention has been given to the polar region, but in no case has there been any indication of bodies that might be taken for

[5] Zeitschrift für wiss. Zoölogie **60** : 543–688.

centrosomes, although the cytoplasmic granules may appear in this region as well as in all other portions.

Although irregular in outline, in the daughter nuclei the chromosomes remain more or less distinct in Symplocarpus, and connected to one another by linin threads (*fig. 9*); while in Peltandra the chromosomes are more closely united into a dispirem ribbon, and not readily differentiated (*fig. 21*). In neither case is there any reappearance of the nucleolus before the second division is entered upon, this being in marked contrast with what obtains in certain dicotyledons under study at the same time—especially Bignonia.

In the telophase of division in Peltandra, the kinoplasmic fibers largely disappear from the middle portion of the cell after the formation of the cell plate has begun, and these fibers are then found to be abundantly concentrated at the periphery. They pass around in the plane of the long axis of the nucleus, entirely surrounding the latter. They form a complete weft around the periphery of the daughter cells, especially adundant in the equatorial region (*fig. 21*). When the development of the cell plate is complete, and the two daughter cells are distinct, these radiations are separated at the extreme edge; and from that point they radiate as before (*fig. 22*). They are evidently concerned in the formation of an independent wall, even in the two-cell stage.

THE SECOND DIVISION.

After the first division in Symplocarpus, some peculiar condition renders staining a very difficult process. The safranin-gentian-orange gives a diffuse pink in the general cytoplasm, and the chromosomes appear indefinite in outline. Iron haematoxylin often works to better effect if the sections are deeply stained and much decolorized. In this stage it is necessary to make the sections very thin. The difficulty in staining persists until the microspores become free, and then again the material is favorable. The second division has not been studied in Peltandra.

With the disappearance of the nuclear membrane, there is formed a clearly defined multipolar spindle, whose general axes from the first are perpendicular to the plane of the first division. This readily becomes bipolar in the usual manner. The form of the chromosomes as arranged on the nuclear plate is more or less quadranglar in front view, and oblong as observed from the poles. Viewed axially, there is an evident line of splitting, and on fission there result short, rod-shaped, daughter segments. The character of this division, of course, depends largely upon the character of the first division, and the doubt involved in this first division cannot now be cleared up.

After the formation of the four nuclei denoting the future microspores, there is a slight reappearance of spindle connections between the daughter cells, or, rather, secondary spindles are differentiated with very delicate spindle fibers.

THE MICROSPORE.

Upon the dissolution of the mother-cell membrane, the tapetal cells become free, and wander in between the maturing microspores. Coming in contact with these forming microspores, the tapetal cells lose their identity as distinct cells, forming a general protoplasmic stratum, in which the nuclei persist for some time. Imbedded in this nourishing layer, the microspores rapidly increase in size, at the same time assuming a thicker wall.

When first freed from the mother-cell membrane, the nuclei of these microspores do not show a single definite nucleolus. Instead, there are usually several irregular masses, which constitute the chromatin content. With the maturity of the spores, a single large nucleolus, more or less spherical in form, is evident, although there may be one or more much smaller bodies staining similarly.

DIVISION OF THE MICROSPORE NUCLEUS.

In neither plant has the spirem stage of this division been studied in detail. In Symplocarpus the earliest preparations of

the spirem show numerous distinct chromatin granules on a comparatively short ribbon. The ribbon soon becomes much thickened, with many sudden bends and irregular twists, larger chromatin masses being evident at definite places. By its bendings the whole ribbon seems to be marked off into definite segments, as in *fig. 10*. At this stage often the connection of the ribbon with the nucleolus may be seen. Immediately preceding actual segmentation, as well as afterward, each forming segment has its chromatin massed toward the ends. A longitudinal splitting of the segment is then evident, thus somewhat imitating a characteristic of heterotypic division. On separation, or complete segmentation, the form of the chromosomes is that of a double half link.

With approaching division, the nuclear cavity increases somewhat in size, and the chromosomes are in the vicinity of the nuclear membrane. The nucleus is in a position near that wall, along which, apparently, the microspore was adherent in the mother cell. With the gradual opening of the network forming the nuclear membrane, kinoplasmic threads enter the nuclear hollow largely from the region of the greatest cytolasm; and no previous radial arrangement of these threads is noticeable.

In the forming spindle of the microspore nucleus, an interesting variation from the normal type of multipolar spindle prevails. The fibers readily take up a position more or less perpendicular to the wall near which the nucleus is located. These fibers arrange themselves in contact with this wall at many points, or in a subpolar manner. At the opposite or free end there are at first, also, false poles. There is then a multipolar spindle in an axial plane. Finally, at the free end, the clusters are usually drawn together into a single pole, or what is approximately a single pole. The complete spindle is thus truncated at one end, and more or less conical at the other (*fig. 11*).

When arranged in the nuclear plate, the ends of the chromosomes point outward, and on account of the loop form there appear to be more chromosomes in the periphery than are really present. As in the case of the pollen mother-cell divisions,

the chromosomes are loosely arranged throughout; and the metaphase proceeds with separation of the daughter segments at the split previously indicated. In the anaphase, when drawn to the fixed pole, the chromosomes are arranged as if in close contact with the membrane adjacent.

From the position of the microspore nucleus just previous to this division, it is to be noted that the spindle is further peculiar on account of its orientation in a plane perpendicular to the greatest mass of protoplasm. There is some evidence that the nucleus of the microspore constantly remains in the vicinity of that wall of the microspore which was in contact with the other spores in the group of four, yet certainly not in contact with this wall. Since this wall is usually in a plane perpendicular to the greatest mass of protoplasm, this may partially account for the constant orientation of the spindle. The free pole of the complete spindle occupies approximately the center of the spore, hence the axis of the spindle is about equal to half the short diameter of the spore. In this division the sudden disappearance of the large nucleolus is a matter of some interest, in connection with other observations previously given upon this organ. In some cases large fragments of nucleolar-like substance seem to be entangled in the fibers of the developing spindle, and in several cases a large mass of this material has been found at the free pole, and apparently held between the fibers.[6] Moreover, in accordance with the observations of many others, I noticed only a few deeply staining granules in the cytoplasm previous to the disappearance of the nucleolus; but in the anaphase and telophase stages of division they are especially abundant in the vicinity of the free pole. They do not, however, disappear with the formation of the daughter nuclei, persisting for a time, but disappearing almost entirely before the pollen grain is mature.

The general effect of the division of the microspore nucleus is well known, but some details may be mentioned, particularly

[6] DEBSKI: Beobachtungen über Kerntheilung bei *Chara fragilis*. Jahrb. f. wiss. Botanik **30**: 227. 1897.

concerning the cell division. Invariably a cell plate separates the daughter nuclei, and the concave side of the forming membrane is toward the small, generative nucleus (*fig. 12*). Generally the generative cell is cut off by a distinct wall, and in the pollen grain two principal types of generative cells are seen. In the first place, the strongly convex membrane necessitates the formation of an oval cell, and the large vegetative cell grows closely around it. The smaller cell is, as it were, drawn into the protoplasm of the surrounding cell, and thus the former becomes more nearly spherical in outline. The generative cell at first contains considerable cytoplasm, but this is gradually lost, although the shrunken wall remains, as in *fig. 13*. Whether taken into the protoplasm or not, the space between the walls of the vegetative and generative cells is evident, and remains surrounding the generative cell as a distinct court. On the other hand, the generative cell may remain closely adherent to the wall for some time, and in this case it is sometimes oval, but usually distinctly fusiform or lens-shaped, sooner or later. The fusiform cell usually remains attached until germination of the pollen grain. As before, the cytoplasm largely disappears, and there remain only small courts on each side of the oblong nucleus. In some cases the nucleus itself becomes fusiform, and it is difficult to distinguish the enveloping walls.

In the division of the microspore nucleus in Peltandra, the spirem ribbon is longer and more complicated than in Symplocarpus; and on segmentation the chromosomes are longer. As the daughter segments pass to the pole, they are distinctly U or V-shaped, as in *fig. 24*. The spindle is formed much as in Symplocarpus, being somewhat multipolar at the pole which is in contact with the wall layer; and at the free pole the apices do not closely converge, as shown in *fig. 23*. In Peltandra, moreover, it is not such an open question as to the influences determining the position of the nucleus in the mature miscrospore. A large vacuole occupies much of the contents of the microspore, and this seems to be an efficient means for the orientation of the nucleus in such a position that one pole of the spindle

may be in close contact with the wall of the spore; the resulting division gives again the characteristic difference in the size of the cells. In this case, however, the plane of the spindle is usually in the plane of the long diameter of the spore.

With the orientation of the microspore spindle so fixed as it is in these plants, it is easy to explain the dissimilarity in the size of the resulting cell-bodies. In this division, moreover, there is evidently equal division of the chromatin, as there is in all normal karyokinesis. The smaller nucleus resulting can have nothing to do with the chromatin content, and must depend upon its relation to the smaller cell body. From the zoological point of view, unequal segmentation as a factor in diffentiation is fundamental, and various speculations have been entered upon as to the cause of unequal division of the cell-body. Wilson[7] prefers Conklin's[8] view, that the cause lies in some relation between the karyokinetic figure and the cell body in which it lies. The inequality in the sizes of the nuclei in the pollen grain, moreover, might be explained largely from the unequal cell divisions. In those cases, however, of division in the microspore where it is reported that no cell wall is formed, we must assume that at least a transient plate or membrane must be formed in order to regulate the sphere of activity about each nucleus, and hence, probably, the size of each nucleus.

In Symplocarpus there was no division of the generative nucleus in the pollen grain. Germinated pollen was obtained in a few hours by sowings on pith in 3 per cent. sugar solution. On a moist day I also found germinated pollen in the bract of the flower, but this is unsatisfactory to work with on account of the difficulty of taking it through the embedding process. I did not secure spindle stages in the division of the generative cell, but enough was secured to show that division occurs soon after the nucleus passes into the pollen tube. The vegetative nucleus usually passes into the pollen tube first and does not deteriorate until after the division of the generative cell. The generative

[7] The cell in development and inheritance 275.

[8] The fertilization of the ovum. Biol. Lect. Marine Biol. Lab. Boston, 1894.

nucleus passed into the pollen tube while still inclosed within its cell membrane ; and several preparations showing stages following division indicate that a membrane surrounds the two nuclei for some time (*fig. 14*). From the same figure it will be seen that the chromosomes of the daughter nuclei have not formed a dispirem, but remain for some time in the segmented form. What the form of these nuclei may be at a later stage, I have not been able to determine.

NOTES ON MATERIALS AND ON METHODS.

Collections.—In Symplocarpus I failed to secure any material earlier than October 1, and at this time the definitive microsporic archesporium was formed, and the nuclei of the pollen mother cells were well in the resting condition. The resting condition was found as late as January 1 ; but much of the material collected during late December and early January was in synapsis. Division of the pollen mother-cells occurred abundantly during the first warm days of February. Although a true spike, the order of maturity of the anthers in Symplocarpus is acropetal, in spite of the fact that the receptivity of the stigmas is often synchronous. It is essential in collecting material to make an examination of a median anther to ascertain the general stage of development, although in exceptional cases there may be great variation in a single spike. It is not uncommon to find all stages from an early spirem to a late stage of division in the pollen mother-cells. However, the development seems to go somewhat in waves. Usually all are in synapsis at the same time ; then there is a rest after the second division of the pollen mother-cells, and there is no actual division of the microspore nucleus in any anther until at least the spirem stage of this division has been reached by all.

For the best penetration of the fixative, it is necessary to open the anthers, and this is readily effected wholesale by shaving off a little of the outer portion of the spike. The stamens may be again cut off next to the surface of the axis, and readily separated from the parts of the perianth. After fixing twenty-four

hours, the material was washed for a few hours, and then carried through several grades of alcohol to 70 per cent. It was necessary to decolorize with peroxide of hydrogen, and this can be done advantageously by mixing it with alcohol to a strength of 70 per cent. alcohol.

After dehydration with absolute alcohol, cedar oil has been used as an infiltrating agent. A small quantity is poured into the absolute alcohol, and into this the material soon sinks. When clear, a change to pure cedar oil is made for a number of hours, then into a mixture of paraffin and cedar oil, and finally into pure paraffin for a few hours. A change of the pure paraffin is well, in order to rid the tissues of all cedar oil; for a trace of the latter may cause electrification and crushing in section cutting.

Staining.—A modification of Flemming's triple stain of safranin, gentian violet, and orange was relied upon primarily, but quite generally supplemented with iron haematoxylin and orange. In using the triple stain, various safranins were used; but with Symplocarpus a final effect of the safranin was of no value, and it was quite generally discarded for a double stain of gentian violet and orange. Ehrlich's gentian violet was used, and for some stages short staining with the strong solution would suffice; but in cases where there was difficulty in staining the spindle fibers, or cytoplasmic radiations, it was found much better to stain from eighteen to twenty-four hours in a tumbler of water containing about one cubic centimeter of the gentian. The orange was used from a fraction of a minute with spindle stages to several minutes with mature pollen grains. After the orange, I have found it advisable to wash out most of the surplus gentian in absolute alcohol, or rinsing at first with 95 per cent. alcohol, if desired. Differentiation with clove oil was effected by simply dashing the slide with the oil, since a much longer action often causes a loss of detail. The sections are then fixed and cleaned in bergamot oil before mounting. In some cases it is well to dash with bergamot oil before differentiating the orange with clove oil, especially in stages where the gentian is

very readily lost; for in such stages clove oil must be used very cautiously. In plants whose cytoplasmic structure is very loosely netted, these precautions are unnecessary. In general, I have secured better differentiation of the chromosomes, or rather more distinct outlines, by using strong gentian. On the other hand, spindle effects are usually superior from the use of dilute stains. Considerable experimentation is necessary in order to determine what is the best method of procedure for each plant studied; but for this purpose time may well be afforded.

Iron hæmatoxylin gave some brilliant results where the Flemming combination was least effective, as in the second division of the pollen mother-cells of Symplocarpus, and especially in stages of the maturing pollen grain and of the dividing microspore nucleus. It was found well to keep the sections in the iron alum for more than an hour, and then to stain in hæmatoxylin from twenty-four to thirty-six hours, from which a better differentiation results. Otherwise, it is difficult to get such a distinct effect in the chromosomes when the cytoplasm is properly decolorized.

BOTANICAL DEPARTMENT,
CORNELL UNIVERSITY.

EXPLANATION OF PLATES I AND II.

PLATE I. Symplocarpus fœtidus.

All figures drawn with the aid of the camera lucida, at 12 ins. projection, tube length 155 mm; nos. 1–12, 14–19, and 21–24 with comp. ocular 8 and $\frac{1}{18}$ hom. imm.; no. 13, ocular 3 and objective as before; no. 20, comp. ocular 18 and objective as before.

FIG. 1. Nucleus in synapsis; peculiar orientation of kinoplasm in the cytoplasm.

FIG. 2. Spirem stage in which the chromatin disks are prominent on the linin framework.

FIG. 3. Early development of the chromosomes; chromatin appearing in tetrad-like groups; fusiform nucleolus.

FIG. 4. A segmentation stage in which loops and X and Y forms are abundant.

FIG. 5. Forms of nucleoli not infrequently observed.

FIG. 6. Multipolar spindle with only a few prominent poles.

FIG. 7. Complete spindle of the first division, showing the form of the chromosomes on the nuclear plate; 7*a*, a polar view of chromosomes as arranged on nuclear plate.

FIG. 8. Pollen mother-cell during an early anaphase of division.

FIG. 9. Daughter nuclei with chromosomes distinct, but irregular in form; early stage of cell-plate formation.

FIG. 10. Microspore nucleus in an early stage of segmentation.

FIG. 11. Peculiar spindle of the microspore division.

FIG. 12. Daughter nuclei resulting from the division of the microspore nucleus.

FIG. 13. Pollen grain with small generative cell surrounded by its court, but free in larger vegetative cell.

FIG. 14. Pollen tube showing sperm nuclei and deteriorating vegetative nucleus.

PLATE II. Peltandra undulata.

FIG. 15. Nucleus in spirem stage.

FIG. 16. An early stage in the segmentation of the chromosomes.

FIG. 17. Radial arrangement of kinoplasm in pollen mother-cell; chromosomes differentiated.

FIG. 18. Pollen mother-cell with kinoplasmic weft in the vicinity of the nuclear membrane at the time when the latter begins to disappear.

FIG. 19. A stage in the development of the rather indefinite multipolar spindle; chromosomes occupying a central position.

FIG. 20. Complete spindle of the first division, also showing the separation of the segments.

FIG. 21. Daughter nuclei resulting from the first division of the pollen mother-cell; cell plate forming at the periphery.

FIG. 22. Daughter cells showing the peculiar arrangement of the kinoplasm at the completion of the cell division.

FIG. 23. A division of the microspore nucleus, showing the characteristic spindle.

FIG. 24. An anaphase stage in the division of the microspore nucleus.

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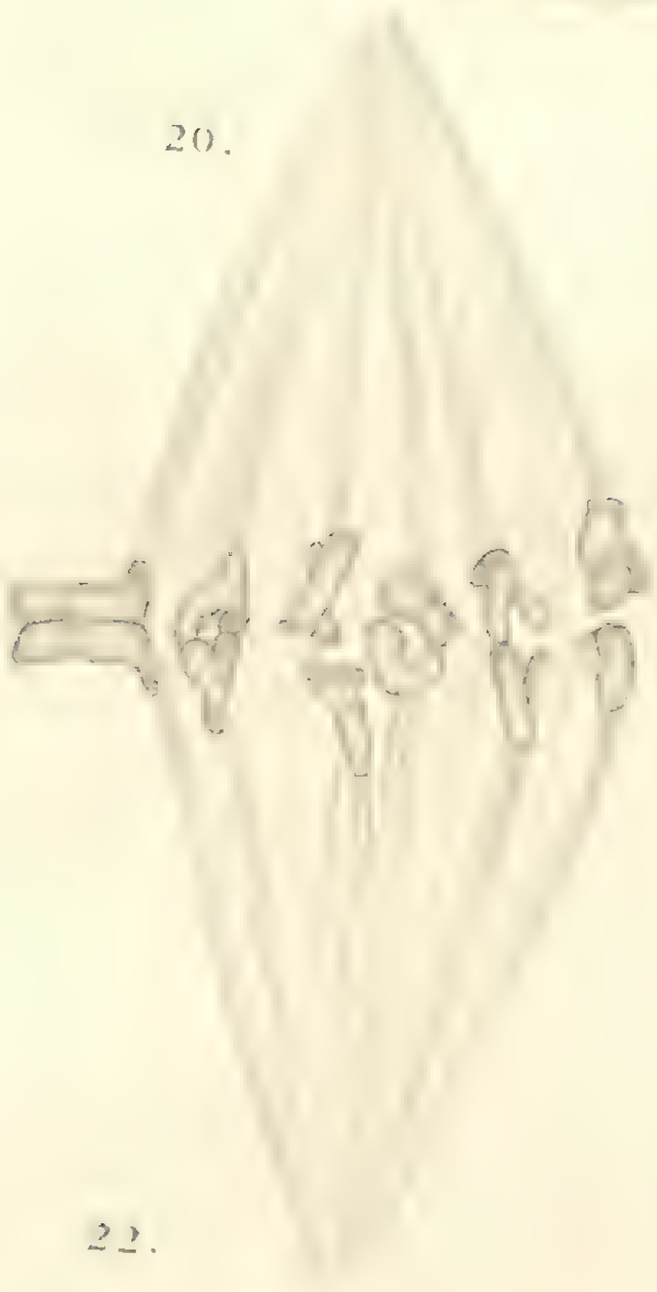

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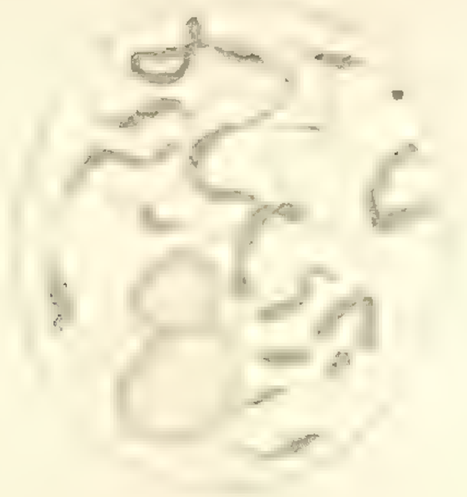

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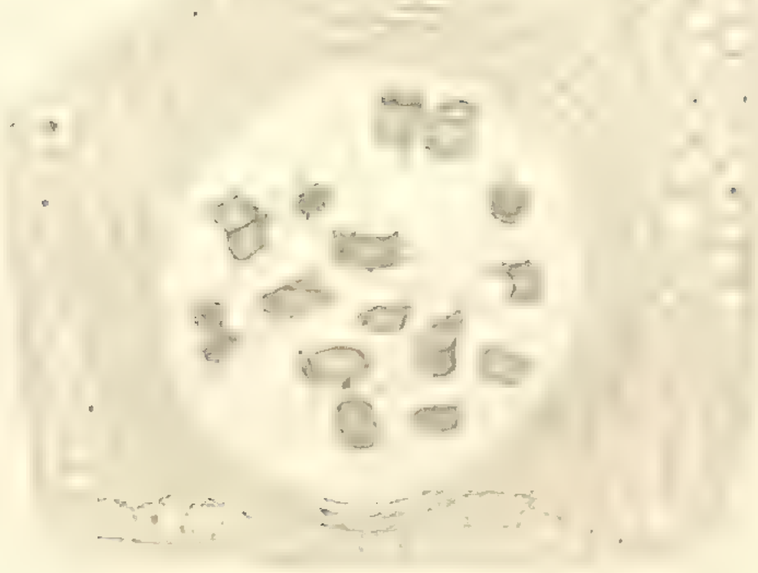

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DUGGAR on PELTANDRA

A CONTRIBUTION TO THE LIFE HISTORY OF SILPHIUM.

CONTRIBUTION FROM THE HULL BOTANICAL LABORATORY. XVII.

WILLIAM DAYTON MERRELL.

(WITH PLATES III–X)

INTRODUCTION.

THE flowers of Compositae are favorable for morphological study, in that several closely connected stages may be obtained in a single section. The broad outlines of the organogeny of the flower were early discovered, and it has only remained for later investigators to examine the more minute details.

Aside from an interest in the family as being the highest among dicotyledons, the division of labor among the flowers of a head deserves attention. This is carried so far in Silphium that the ray-flowers are ovulate and without stamens; while the disk-flowers are staminate and without ovules, the style never forking. It might be expected that some transitional stages in the abortion of stamens or of ovules could be found, and the present study was undertaken with that in view. The results obtained in this particular were very meager, but the investigation led to the discovery of several unexpected phenomena, which are herewith presented.

MATERIAL AND METHODS.

The material was collected during the summers of 1896, 1897, and 1898, in the vicinity of Chicago. Unfortunately, most of the collections had to be made in the latter part of the day, and this probably accounts for the small number of cells found in process of division. Even in the youngest buds it was found to be advantageous to pick off the outer involucral scales, partly

because they interfered with the rapid penetration of the fixing fluid, but more especially because their brittleness very quickly spoiled the edge of the microtome knife. The older akenes, containing embryo-sacs or embryos, were picked off separately, and cut one at a time.

For fixing the early stages of development, as well as the mature embryo-sac structures, the best results were obtained with a 1 per cent. solution each of chromic acid and acetic acid. A weaker solution, containing 0.7 per cent. chromic acid and 0.3 per cent. acetic acid, worked well, especially when the specimens were first dipped for a moment in alcohol. Flemming's weaker solution was tried for killing embryo-sac stages, but was abandoned as being unnecessary. A saturated solution of picric acid in 70 per cent. alcohol, with a small addition of acetic acid, was frequently used, and was found to be by far the best for all stages of embryos, as it penetrated the hard ovary wall more quickly. After dehydration the objects were brought through xylol into paraffin, and cut in serial sections.

Delafield's haematoxylin, either alone or followed by erythrosin, was found to be the best stain for floral development stages and for embryos. For embryo-sacs, safranin-gentian-violet, cyanin-erythrosin, and Heidenhain's iron-alum-haematoxylin were used; also a combination of fuchsin and iodin-green. For the nuclei within the pollen grains, safranin-gentian-violet, and especially the iron-alum-haematoxylin, gave good results.

The following five species of Silphium, growing near Chicago, were examined, a more or less complete series in each being made: *S. integrifolium* Michx., *S. trifoliatum* L., *S. terebinthinaceum* L., *S. laciniatum* L., and *S. perfoliatum* L. Most of the statements apply to all these species, hence no attempt will be made to separate them in the account, excepting in cases where points of specific difference are under discussion.

My acknowledgments are due to Professor John M. Coulter and to Dr. Charles J. Chamberlain for great assistance rendered during the course of the work.

ORGANOGENY OF THE FLOWER.

On account of the difference in the development of the disk and ray flowers, it is necessary to consider the two separately. It has been found, also, that a clear understanding of the sequence and relations of the organs in the disk flowers assists greatly in the interpretation of the more irregular development of the ray flower.

Disk flowers.—The earliest appearance of the disk flowers upon the receptacle is shown in *fig. 1*, the broader protuberance (*d*) being the receptacle of the individual flower, and the narrower one (br_1) the subtending bract. A second bract (br_2) is just appearing. Just before the appearance of the first floral organs the receptacle is of the form shown in *fig. 2*, d_2, being somewhat broader than high, and very symmetrical in outline.

The outline of the receptacle soon becomes angular by the upward growth of a marginal ring (*fig. 2*, d_1, *fig. 3*), which is the beginning of the corolla tube. In *fig. 4* the corolla tube has begun to curl inward over the top of the flower, and an inner set of five hemispherical protuberances (*st*), the young stamens, have appeared. The appearance of the carpels (*k*, *figs. 5*, *6*) is accompanied by a broadening of the receptacle, which regains its original proportions as the stamens and carpels acquire a more erect position (*figs. 7*, *8*).

In *figs. 7* and *9* a notch may be seen on each side at the base of the corolla, just above an annular swelling. This ring marks the position of the calyx, which soon appears (*fig. 10*, *pa*) as a rudimentary pappus of two or three whorls of short hairs, each hair consisting of about three cells (*fig. 11*). The nectary consists of a ring around the base of the style (*fig. 9*, *n*).

Martin's account for Aster and Solidago (19) agrees in a general way with the account of Silphium here given. However, he finds the calyx in those forms arising much earlier, in fact almost simultaneously with the stamens.

It is well known that in many Compositae the base of the style is spirally coiled, and the straightening of this spiral at maturity constitutes the stylar thrust by which the pollen is

brushed out of the stamen tube. My preparations show no such device in Silphium. A comparison of *figs. 9, 10, 11* shows that while at one time the style is actually longer than the stamens (*fig. 10*), the stamens soon overtake the style again (*fig. 11*). As this is in a flower where the pollen-mother cells have reached a late synapsis stage, and the maturity of the pollen follows rapidly, it would seem hardly probable that the style could become coiled before the dehiscense of the anthers. The stylar thrust seems to be accomplished rather by an actual increase in the length of the style, partially, at least, by mere cell elongation.

It will be seen that there is no trace of an ovule, or even of an ovary, in the disk flower. In other respects the resemblance to Helianthus (Sachs) is quite close.

Ray flowers.— The ray flowers occupy about two turns of a spiral upon the receptacle. As the individuals of the two rows alternate with each other, only one can ever appear in a single radial longitudinal section of a head. Moreover, in serial sections, never more than two rays, one each from the inner and outer rows, are cut near enough to the radial plane to be valuable for study. It will be seen that in the form of the young ray flower Silphium shows a very close resemblance to Aster and Solidago, especially when, as happens in the great majority of cases, rudimentary stamens are present.

The ray flowers of the outer row (*r*, *figs. 1, 2*) are subtended by bracts of the involucre, which are so closely folded over in the bud as to distort the young flower for a considerable period. This compression on the anterior side is plainly visible in *fig. 12*, where the corolla is starting, and is still noticeable in *fig. 13*, where the stamens (*st*) are just appearing. *Fig. 14* shows in addition the young carpels (*k*), and *figs. 15, 16* show the beginning of the ovule (*ov*). At about the stage shown in *fig. 14* the corolla tube begins to grow more rapidly on the anterior side, and is thus pushed away from the subtending bract. The opening of the tube is gradually made smaller by the growth of its lateral edges, which finally lap past each other and give rise to such appearances of the corolla as are shown in *figs. 18–24*,

dependent upon the age of the bud and the exact portion of these folds appearing in the section. This infolded portion finally unrolls to form the limb of the corolla.

Although the stamens never reach maturity in the ray flowers, they are to be found in the great majority of young flowers. While one may be in doubt as to their identity in *fig. 13*, conclusive proof of their presence is found in *figs. 14, 15, 16*. *Fig. 20* shows a single anterior stamen in median section, whereas *figs. 18, 19*, of almost the same age, show no such rudiment, even in lateral sections. The significance of this last statement is seen upon an examination of *fig. 21*, in which only the two carpels (*k*) appear in a median section, while, in a lateral section (*fig. 21, a*), two stamen rudiments (*st*) are found. In one head, two flowers were found, each showing a single stamen which had developed to the pollen-mother cell stage (*fig. 24*).

The ovary arises as a cavity below the carpels, soon widening at the base as the ovule becomes visible. The *Anlage* of the ovule appears slightly toward the posterior side of the base of the ovary (*figs. 15, 16*), grows obliquely upward (*figs. 18, 19*), and soon becomes erect (*figs. 20, 21*). In the last figure cited, the apex of the nucellus is already pushed slightly to one side, but hardly enough to warrant the statement of Sachs (**14,** p. 572) that the nucellus, when first visible, stands laterally below the apex of the funiculus, a mode of development for some anatropous ovules first described by Cramer (*ibid.*), and later called in question, at least for Compositae, by Köhne (*ibid.*). It seems plain that in a stage just earlier than that of *fig. 21*, perhaps in *fig. 20*, the cell which later becomes recognizable as the archesporium occupies an exactly terminal position upon the young ovule; and the bulging on the anterior side, already begun in *fig. 21*, is merely the beginning of the integument, which, growing from now on more rapidly than the nucellus, forces the latter to a lateral position, and finally completely inverts it (*figs. 22–25*).

The often affirmed lateral origin of the ovule is thrown in doubt by the fact that Martin (**19**) relates it by its bundle,

in Aster and Solidago, to the posterior or "upper" carpel. The *Anlage* of the ovule is said to be excentric, and nearer to the posterior carpel, a position which Warming figures for Senecio, but which is hard to explain if, as all the earlier writers agreed, the ovule belongs to the anterior carpel.

I find that the ovule of Silphium is generally posterior in origin (*fig. 16*), but it may sometimes arise anteriorly (*fig. 17*). This fact suggests that the excentric origin of the ovule is of but slight significance, since it may vary in the same species. On comparing the course of the bundles with that described for Aster and Solidago, I find that the axial bundle, instead of ending abruptly just below the edge of the funiculus, passes directly into the ovule (*figs. 24, 26, 27*). Whatever may be the condition in other Compositae, the ovule of Silphium, as shown by its origin and its bundle relations, is the termination of the floral axis, that is, the ovule is cauline. The oblique position of its *Anlage* is correlated with the position which must sooner or later be taken by the funiculus of an anatropous ovule in an ovary of limited size.

It should be noted, in passing, that the bundle does not terminate in the upper end of the ovule, but continues in the integument to a point on a level with the embryo sac (*fig. 27*). This is not in agreement with the recent work of Mlle. Goldflus (27) upon Composite ovules, according to which the bundle ends directly above the chalazal region, and is connected to the antipodals by a strand of elongated conducting cells.

Nectaries.— It has been suggested that the nectaries of Compositae are modified stamen rudiments. The disk flower of Silphium offers no conclusive evidence for or against this view, as the nectar disk occupies a position within the stamen whorl, and might be interpreted as consisting of the confluent rudiments of an inner whorl of stamens. The nectary in the ray flower is also a ring, less prominent than in the disk flower, but even more closely related to the base of the style. The general absence of maturing stamens here makes a comparison of the two rather difficult. But in the two cases of older stamens

which I found, the nectary was in each case below the stamen (*fig. 24*). It is hardly conceivable that the nectary of the ray flower is formed from an outer stamen whorl, not yet completely lost in the genus, while in the disk flower it comes from an inner set which is absent in all the tetracyclic Sympetalae. It is much more reasonable to regard the nectary as an organ of independent origin.

DEVELOPMENT OF THE MEGASPORE AND EMBRYO SAC.

When the ovule has reached the stage shown in *fig. 22*, the hypodermal archesporium is easily recognizable at the end of an axial row of cells (*fig. 28*). Its cytoplasm is finely granular, and its nucleus has already left the resting condition, showing a continuous spirem thread along which the chromatin granules are arranged. *Fig 29*, from an ovule of about the age of the one in *fig. 23*, shows the nucleus with a prominent nucleolus and eight bodies of a different staining reaction, the chromosomes. There is as yet no trace of a spindle. In *fig. 30*, taken from the ovule outlined in *fig. 24*, the equatorial plate is fully formed. A complete count of chromosomes was not possible here, owing to their being so closely crowded together. Six were plainly visible, and a comparison with *fig. 29*, and with the corresponding division of the pollen mother cell (*fig. 54*), leads certainly to the conclusion that eight is the characteristic reduction number. I have made no accurate count of the chromosomes in other tissues, but dividing nuclei found in the large tapetal cells appear to have many more than eight, probably sixteen.

Guignard (15) describes the reduction division in the ovule of *Allium ursinum* as occurring in the archesporial cell, which here produces a row of four cells, the innermost of which develops into the embryo sac. A similar condition has been reported by Strasburger for *Allium fistulosum* and *Helleborus foetidus* (16). Such a row of four cells is formed in Silphium (*fig. 31*), as indeed in all the Compositae which have been examined. In the determination of the homologies of the cells thus produced, as well as that of the original hypodermal cell, the reduction

division is certainly to be regarded as a valuable factor. Considering it, for the moment, as of primary importance, the cell in which it occurs in the ovule is a megaspore mother cell, producing by two successive divisions four megaspores, the innermost of which germinates. The presence of a tapetal cell would be determined, not by its size or shape, but by its being cut off before the reduction division occurs.

Many botanists, however, look upon the linear arrangement of the four cells, and the entire absence of any internal cell division in their formation, as serious objections to this view, and prefer to call each of the four a spore mother-cell, of which the fertile one develops directly into the megaspore. This would make each of the four cells in a form like Silphium the homologue of the single fertile cell of Lilium. But to the writer, the linear arrangement of the four cells finds a parallel in the "zonate" method of division in the tetraspores of some Rhodophyceæ; and it seems but natural that a process of "rejuvenescence" should be abandoned in the development of a spore which is not to be shed, but germinates *in situ*. The condition found in Lilium would then be but the extreme abbreviation of the story, the archesporial cell itself developing into the megaspore.

The successive stages in the development of the megaspore, accompanied by the destruction of the potential megaspores, are shown in *figs. 31–37*, and present no essential deviations from the process as ordinarily described. The megaspore encroaches but slightly upon the cells of the chalazal region, apparently finding less resistance to growth in the opposite direction. This results in a stretching of the cells of the nucellus, which consists of but a single layer of cells, the epidermis, surrounding the row of megaspores; and finally the rupture of the nucellus (*fig. 36*), part of which may be carried downward on the tip of the growing sac (*fig. 37*). The greater part of the sac, from this time on, lies free in the space between the funiculus and the integument. At its base may usually be seen the remnants of the broken nucellus.

The amount of protoplasm in the developing sac is comparatively small, frequently resulting in the presence of very large vacuoles. It will be seen also that the enlargement of the sac, the division of its nuclei, and the destruction of the surrounding cells, do not proceed at the same rate. Thus, in *fig. 34* the two nuclei have not left their position in the central strand of protoplasm in which they were formed, while there is no trace of the potential megaspores, and the nucellus is stretched almost to the point of breaking; in *fig. 35*, on the other hand, the nuclei are already widely separated, whereas the sac itself is smaller than in *fig. 34*, the remains of the potential megaspores are still recognizable, and the nucellus itself is in a fairly good condition.

The structure of the mature embryo sac may perhaps best be described by taking that of *S. integrifolium* as a type, and comparing the other species with it. As shown in *fig. 38*, the sac is several times longer than was the nucellus. It attains its greatest diameter at about one third of the distance from its micropylar end, and from this point it tapers quite uniformly toward the antipodal region. The egg apparatus occupies about the outer quarter of the sac. The synergids (*sy*) always lie, the one anterior to the other, in one side of the sac, the opposite side being occupied by the oosphere (*o*), which is attached well up toward the apex of the sac. It is quite common for each synergid to have a large vacuole in each end, with the nucleus lying between them. In *fig. 38* the egg lies above the synergids, almost covering one of them, whose projecting margin is shaded deeply for the sake of distinctness. The reconstruction of the drawing from adjacent sections also made it necessary to represent the vacuoles and nuclei of the synergids as if showing through the protoplasm of the egg.

The oosphere shows a large vacuole in its broad upper portion. Its nucleus is larger than those of the synergids, and contains a very fine chromatin network in resting condition, and a large and often vesicular nucleolus. After the fusion of the polar nuclei, which occurs near the middle of the sac (*fig. 37*), the primary endosperm nucleus approaches the egg apparatus,

and is frequently to be found crowded close into the angle between the egg and the synergids, as in *fig. 38*. It is much larger than the egg nucleus, but in other respects resembles it quite closely. Its nucleolus usually contains one large and several smaller vesicles. The body of the sac is occupied by a large vacuole.

The antipodal cells are generally three in number, separated by walls and arranged in a row, the innermost being much the largest. The Compositae have long been known to exhibit great variability in the antipodal region, a multiplication of cells and nuclei being reported in *Senecio aureus* by Mottier (**20**), in Aster and Solidago by Martin (**19**), and in *Aster Novæ-Angliæ* by Chamberlain (**23**). The same variability has been seen, to a certain extent, in Silphium, in all the species studied. The wall may be lacking between two of the three nuclei, giving but two cells (*fig. 39*), either or both of which may show strong indications of direct nuclear division. Again, the nucleus may divide in any one of the three cells (*figs. 40, 41*). Finally, in one case, seven antipodal cells were found, containing eight nuclei, with indications of amitotic division (*fig. 42*).

In a recent paper by Mlle. Goldflus (**26**), already referred to, it has been shown that the antipodal cells in the Compositae possess at times a digestive function, and in other forms serve to conduct food from the ovule to the growing sac with its embryo. All the evidence goes to show that in Silphium these cells are conductive, rather than digestive. It is equally clear that in those forms where the antipodals burrow back into the chalazal region, a fact which may perhaps be correlated with the reduced size of the nucellus, the surrounding cells must be destroyed by the action of a ferment secreted by the cells of the encroaching tissue. The possession of either of these functions is claimed by the author to be inconsistent with the interpretation of the antipodal cells as a vegetative or prothallial region of the gametophyte. But it must be admitted that the most natural function of the vegetative, as distinguished from the reproductive, region of a prothallus, is that of nutrition, of which digestion and

conduction are but two important phases. The view that the antipodals are homologous with the vegetative portion of a pteridophyte prothallus is strengthened, therefore, rather than overthrown by the discovery of the rôle which they play in the nutrition of the embryo sac.

I have reserved one feature in connection with the egg apparatus for a special consideration, namely, the peculiar cap which is usually to be found upon the micropylar end of the sac. Its ordinary appearance is as in *fig. 38*. It is frequently striated, and always shows a rift or superficial groove, which cannot be related, however, to the line of contact between the synergids. The material of which the cap is composed stains deeply with all the stains used, but when lightly stained the outline of the tip of the sac can be seen within it, showing that the cap is not a part of the synergids. This fact precludes the possibility of its being a filiform apparatus, and I have been led to the conclusion that the cap represents the remnant of the nucellus, which may often be broken in pieces, as in *fig. 37*, but which, in most cases, is pushed forward by the sac and remains perched, calyptra-like, upon its apex. This explanation was first suggested by the form of the nucellus tip (see especially *figs. 32, 35*), and seems to be the only possible interpretation of the condition seen in *fig. 43*, where the cap has evidently continued its growth and become highly vacuolate. Finally, in *fig. 44*, from a preparation poor in other respects, the cap consists of four cells in section, the walls and two of the nuclei still being visible.

The above description of the embryo sac of *Silphium integrifolium* will apply very well to *S. trifoliatum*, *S. terebinthinaceum*, and *S. laciniatum*, the chief differences being in matters of size and proportions, and hardly deserving special mention. The peculiarities of the antipodal and micropylar regions are illustrated from *S. integrifolium*, because its greater abundance, together with its being easier to kill and section, encouraged a more extended study. But abundant evidence was obtained showing that the same peculiarities exist in the other species,

and their apparently greater uniformity is probably due to their having been less fully investigated.

S. perfoliatum presents a type of sac quite different from the other species studied (*fig. 45*). In size it agrees quite closely with *S. trifoliatum*, these two species having larger sacs than the other three. The synergids are of a form peculiar to this species, and resemble more closely those figured for other Compositae. They are slender and pear-shaped, usually without vacuoles, and with the nucleus near the inner end. Their outer ends are long, and filled with a very deeply staining protoplasm. Their outline can be followed very easily inside the membrane of the sac, thus affording indirect evidence in confirmation of the claim that the cap found upon the tip of the sac in the other species is not a part of the synergids, but lies outside the sac.

No attempt has been made to do cytological work in the embryo sac, as the difficulty of fixing the material quickly, due to the hard tissues of the ovary wall, rendered practically unavoidable an amount of shrinkage which, though slight, was sufficient to blur the finer cytological details. The general appearance of the oosphere and primary endosperm nucleus has already been described. The drawings are not intended to do more than to show the structure of the nuclei more or less diagrammatically. There is evidence that the egg nucleus leaves the resting condition before fusion with the male nucleus occurs.

The primary endosperm nucleus in *S. integrifolium* has an average diameter of 15 μ, its nucleolus being 6–8 μ; the oosphere nucleus averages 9 μ in diameter, with a nucleolus of 3 μ. The sac itself is about 220 by 40 μ. In *S. perfoliatum* the endosperm nucleus measures 26 μ, its nucleolus 12 μ; the egg nucleus 17 μ, its nucleolus 6 μ; the sac itself, about 300 by 65 μ.

DEVELOPMENT OF MICROSPORES.

When the young stamen has reached the stage shown in *fig. 7*, the hypodermal archesporial row is distinguishable from the surrounding tissue by the increased size of its component cells and their different staining reaction. A transverse section of

such a stamen shows that its anther is already fusing with those of the other stamens in the flower. In each corner of the anther a single large hypodermal cell is found (*fig. 46*), which soon divides into an outer and an inner cell, which may be called, respectively, the primary tapetal and primary sporogenous cells. If we bear in mind that Goebel applies the term archesporium to the row which we have called primary sporogenous, his statement (*Outlines of Classification, etc.*, p. 363) that in the Compositae the archesporium consists of a single row of cells finds here an easy confirmation (*fig. 47*).

Periclinal walls soon appear in the primary tapetal row, by which it becomes a cell layer. This soon divides into two layers (*fig. 48*), of which the inner is to become the external portion of the tapetum, while the outer divides again to form the "endothecium" and the "middle layer" (*fig. 49*). The tapetal layer is completed by the addition of cells lying between the sporogenous mass and the connective, the whole layer finally consisting of large and usually binucleate cells with densely granular contents. The layer of cells just behind this addition to the tapetum grows to resemble the middle layer, thus completing a second nutritive layer (*fig. 50*). It will be seen that the foregoing account of the origin of the sporogenous cells and their surrounding layers agrees with the early work of Warming.

Meanwhile, longitudinal divisions have occurred in the primary sporogenous row, giving finally a mass of four or five cells in cross section. The appearance of the various layers in longitudinal section is also shown, *fig. 51* corresponding quite closely to *fig. 47*, *fig. 52* to *fig. 49*, and *fig. 53* showing a stage just younger than *fig. 50*. A comparison of *figs. 52* and *53* shows that the rule that when the tapetum is differentiated the pollen-mother-cell stage has been reached is not of such universal application as Guignard claims for it (18). Exception to this rule has already been noted by Miss Lyon in Euphorbia (26). That the sister layer to the tapetum divides to produce the endothecial and middle layers is shown at *x*, *figs. 49, 52*. This division may not occur at all, and in such cases the original

layer forms the endothecium, which then lies next to the tapetum, as in *fig. 54*.

At the time of their first division, the pollen mother-cells are lying free in the cavity of the sporangium, and are perfectly spherical in form. The division occurs simultaneously in all the mother cells in a loculus, and it can frequently be noticed that the two outer loculi are slightly in advance of the inner ones of the same anther. For example, when the spindles in an inner loculus are in an equatorial plate stage, as in *fig. 54*, daughter stars will be found in the mother cells of the outer loculus. As may be seen from the figure just cited, the chromosomes are nearly spherical, and it is very easy to count them, as the spindles lie in all possible directions. In favorable preparations the number eight can be counted repeatedly, even with a comparatively low magnification. Reference has already been made to this as being the reduction number found in the development of the megaspore.

The rapidity with which the second division follows the first may be inferred from the fact that even in the same loculus mother cells may be found, some of which show daughter stars of the first division, while in others one of the daughter nuclei may already have formed the spindle for the next division. The two spindles generally lie across each other, as in *fig. 55*, but they may sometimes be side by side.

We may take *figs. 54, 56, 57, 58*, as showing the stages which may be found in four adjacent flowers along a radius of the head. The spines of the pollen grain appear soon after it is set free from the tetrad. For a time the spore exhibits a large vacuole, but this soon disappears.

While these changes have been taking place the tapetum and middle layer have been disorganizing. In this way a plasma is formed which gradually distributes itself among the pollen grains. The nuclei of the disorganized cells are visible for quite a long time. This plasma finally collects around the spores (*fig. 59*), and is at last encrusted upon them as a sheath (*fig. 62*), exactly comparable to the perinium of a pteridophyte spore.

THE MALE GAMETOPHYTE AND FERTILIZATION.

The pollen germinates in the anther. Three or four places for the exit of the pollen tube are present, and at the time of dehiscence the contents of the spore can be seen protruding slightly from each of them. The two nuclear divisions by which the vegetative and generative nuclei, and the two sexual nuclei, arise, were not followed; but the difference in size and staining reaction in the stages found indicate that there is no deviation from the process as ordinarily described. The generative nucleus (*g*, *fig. 59*) is soon surrounded by a small quantity of hyaline cytoplasm, distinguishable from the more granular protoplasm of the rest of the spore. The nuclei of the two sexual cells (*m*, *fig. 60*) are smaller than the vegetative nucleus. At this stage practically no structure can be made out in any of the nuclei. The male nuclei usually stain less deeply than the vegetative nucleus.

When first formed the male nuclei are approximately spherical, as in *fig. 60, m*. But in later stages their form undergoes a very remarkable change. The nucleus begins to be drawn out at one end, and soon becomes very much elongated. During this process the two nuclei generally lie side by side, and may finally become so long as to reach fully half way around the interior of the pollen grain. Some of the stages are shown in *figs. 61, a–f, 62, 63*. It will be seen that the somewhat sinuous form generally assumed frequently resolves itself into a spiral (*fig. 61, d, e*). This change of form was found in three of the species studied, *S. integrifolium*, *S. terebinthinaceum*, and *S. perfoliatum*, and might possibly have been discovered in the other two had they been as thoroughly investigated upon this point. The structure of the nucleus was very difficult to make out, since, in sections less than 10μ in thickness, so long a body was likely to be cut in pieces; and with this thickness of section the pollen grain would be cut through but once, and the nuclei were seen against a background of deeply staining spore wall. With the most favorable light the nucleus can be seen to consist of a network with extremely fine meshes. The surrounding film of

cytoplasm is not always visible. *Fig. 61, f* shows as nearly as possible the appearance of the fully developed male cell, and brings out also the fact that the sinuous or spiral form is finally lost, and the nucleus is merely slightly bent.

Strasburger and others have figured somewhat elongated male cells in various plants, but no more than could be explained by the need of such a form in order to pass down a slender pollen tube. In one account, that of Golinski (**21**), the male cells of Triticum and other Gramineæ were described as being "not at all unlike an antherozoid of the Characeæ or ferns." He even records the presence of a vesicle, persisting for some time in a loop of the sex cell. Nothing of this kind occurs in Silphium, but, judging by the figures given, the spermatozoid form is here far more pronounced.

Until recently, Golinski's account was the only one which offered any parallel to what has been found in Silphium. Such an association of a composite with the grasses would seem at first to be an absurdity. But it is not a new one, for the Gramineæ stand preeminent among the monocotyledons as the formers of tissue by the antipodal cells, as do the Compositae among the dicotyledons; and if the antipodal cells represent a prothallial region, there is thus a primitive character in the female gametophyte of both groups, matched now by the peculiar form of the male cells.

Nawaschin's recent announcement (**28**) of long, vermiform male nuclei in *Lilium Martagon* recalled a figure published last year by Mottier (**25**), showing a coiled male nucleus lying against the female pronucleus. Fuller confirmation of Nawaschin's preliminary statement has already come from Guignard (**29**), who not only has given us excellent figures, but has extended his observations to several other species of the Liliaceæ. The male nuclei, as he figures them, resemble closely those of Silphium. Their fusion with the polar nuclei, reported by both Nawaschin and Guignard, has not been found in Silphium, which, by virtue of the earlier formation of the definitive nucleus, is not a favorable object for the study of this point.

These recent investigations prove that the occurrence of spermatozoid-like male cells in Angiosperms is not so rare as was once supposed.

The pollen tube passes along the outside of the cap which usually crowns the embryo sac (*fig. 64*), and enters the sac just beyond its free margin. One of the synergids now begins to disorganize, and soons becomes unrecognizable. The other usually persists for a considerable period, lying against, or partly covering, the suspensor of the young embryo. When seen in side view this might easily be taken for a pollen tube, as in *fig. 66*, for example. But a little familiarity with the type soon removes this source of error, as the pollen tube is much more slender. Where the synergid can be seen passing up within the cap, as in *fig. 67*, there is no chance for uncertainty as to its identity. That neither of the synergids may be disorganized until fertilization is accomplished is shown by *fig. 65*.

The recent accounts of fertilization in Lilium, already cited, suggested that a careful study of the behavior of the spiral male cells of Silphium would be very desirable. Unfortunately, the most favorable preparations showing male pronuclei in the oosphere were in *S. laciniatum* and *S. trifoliatum*, the two species in which the elongated cells were not found. Preparations of the other species, showing the nuclei in the tip of the pollen tube, indicate that the sex nuclei have resumed a spherical form. By the growth of the male pronucleus it acquires a close resemblance to the egg nucleus before fusion occurs.

DEVELOPMENT OF THE EMBRYO.

After fertilization the oospore develops a wall, and elongates rapidly. Its proximal end is occupied by a large vacuole, while its distal end is filled with a mass of protoplasm containing the nucleus.

The first wall in the oospore is transverse, as usual, and separates a large proximal vesicular cell from a smaller terminal cell. It will be of interest to note that the primary endosperm nucleus divides before the first wall appears in the oospore

(*fig. 65*). The early divisions of the endosperm nuclei occur more rapidly than those in the embryo, for while there are yet but two cells in the embryo, the endosperm nuclei have passed to their third division, a condition shown in *fig. 66*. The antipodal cells are still to be seen in a small pocket at the extremity of the sac. Their final disappearance does not occur until a considerably later stage.

It is customary to speak of the cell which produces the octants as the embryo cell, and of all the remaining cells as belonging to the suspensor. The term is never strictly accurate, for even in such cases as Capsella the dermatogen and periblem of the root are contributed by the cell below the octants. Again some authors, noticing that the first wall in this "embryo cell" is usually longitudinal, conclude that, conversely, the first longitudinal wall identifies the embryo cell—a definition which breaks down in cases where the octants are formed by a transverse wall followed by two longitudinal walls, as has been claimed by Schwere (**24**) to be the rule for Compositae. If, however, we give to the term "embryo cell" a uniform signification, namely, the cell which produces the octants, we shall at least justify its use as a term of convenience.

Another term of varied application is the word hypophysis, or "Anschlusszelle." In Hanstein's account of the embryo of Capsella (**2**), the cell next below the octants divides by a transverse wall, and its upper half divides again to form the "Periblem-schlusszelle" and the "Dermatogen-schlusszelle,"[1] the latter, by repeated splitting, forming the layers of the root cap. Hanstein applies the term hypophysis sometimes to this original suspensor cell, at other times more particularly to its upper half, thus designating as the "Anschlusszelle" the cell which actually completes the embryo. On the other hand Schwere, for example, applies the term to the cell which is, next below the embryo cell, indeed, but which only partially

[1] Throughout the rest of this account the rather cumbrous words "Dermatogen-schlusszelle" and "Periblem-schlusszelle" will be translated by the terms *dermatogen* and *periblem terminals*, respectively. The fact that they later become the dermatogen and periblem *initials* need cause no confusion when the latter terms are substituted.

corresponds to the cell similarly placed in Capsella; for in Taraxacum this cell produces only concentric layers of dermatogen and periblem, a second suspensor cell doing the same thing, while the root cap is formed by the third cell from the embryo cell. In such a case, the term hypophysis, as applied to a single cell, could be justified only by proving that these three cells arose by the division of an original single cell next to the embryo cell. This, however, has never been done.

As a further preface to the discussion of the development of the embryo, it may be well to state that in the early part of the work the entire ovary was cut longitudinally in the plane of the radius of the inflorescence, in order to determine with certainty the direction of the early divisions in the embryo. Later, the ovules were dissected out, and the direction of the section, whether in the radial or tangential plane, was ascertained from the position of the funiculus.

Passing on now to the second division in the young embryo, we see by *fig. 68* that the two nuclei present may prepare for division at almost exactly the same time. The nucleus of the terminal cell is slightly in advance of the other, as the segmentation into chromosomes has occurred, and the nuclear membrane has disappeared. However, the difference is so slight that we are left without absolute proof as to the origin of such a stage as *fig. 69*. If the terminal cell alone has divided, two interpretations are possible. First, a transverse wall may have arisen in the embryo cell, in which case my *figs. 69, 70, 71* would correspond exactly to Schwere's *figs. 8, 9, a, 9*, respectively, as *fig. 70* is cut in the radial plane and *fig. 71* in the tangential. The second possibility is that the terminal cell in *fig. 69* is the real embryo cell, but marked out by the *second* division in the oospore; and a comparison of *figs. 69, 70* with *72–76* shows that this is actually the cell which produces the octants. This being true, we may now apply the term embryo cell definitely to the terminal one of the three cells in *fig. 69*. It would be an obvious error to give that name to the terminal cell of *fig. 67*, for, according to this interpretation, the latter cell produces

more than the octants. I shall attempt to show that the middle cell of *fig. 69* contributes to all the primary tissues of the embryo, but to change the accepted definition of the embryo cell on this account would result in needless confusion.

A third possible origin for *fig. 69* is that the vesicular cell of *fig. 67* may have divided first. This is not exactly in line with *fig. 68*, but should be recognized as a possible, if not a necessary interpretation. According to this view, the terminal cell of *figs. 67* and *68* would be the same as that of *fig. 69*, and Silphium would agree with other Compositae in having the embryo cell marked out by the first division of the oospore. In the lack of positive evidence on this point it is perhaps best to let this stand as the correct interpretation, at the same time recognizing the possibility that the real embryo cell may be but one of the daughters of the terminal cell of *fig. 68*.

The first wall in the cell producing the octants, or as we may now call it, the embryo cell, is longitudinal, and in the radial plane of the head (*figs. 70, 71*). As the cotyledons of the mature embryo occupy an antero-posterior position in the ovary, it will be seen that this wall does not separate them, but rather cuts each one in two. The cotyledons are not separated until the second series of divisions, in the tangential longitudinal plane, has occurred (*fig. 72*). *Fig. 73* shows an embryo in which the transverse walls followed the first longitudinal, or may even have appeared first; but of this latter there is no proof.

The formation of the octants is soon completed (*fig. 74*), usually by a series of transverse walls in the quadrants of *fig. 72*. The upper octants divide more rapidly than the lower four, and as the two sets differ considerably in their mode of development, it will be easier to treat them separately. We may then go back to trace the development of the cells below the octants.

The first walls in the upper octants are, in most cases, a set of anticlinals. *Fig. 75* shows an embryo with this first anticlinal wall in one of the upper octants. The other three are not yet divided. All of the figures up to and including this one are of whole embryos, with all of the nuclei shown. The remaining

figures are of sections. *Fig. 76* shows one half of an embryo in which all four upper octants have divided. Of the two shown in the figure, the left one has cut off the dermatogen by a periclinal wall, while the right one shows the usual anticlinal wall. The other two of the four show in the adjacent section of the series, each with an anticlinal wall, as in *fig. 77*, which is drawn from another embryo in nearly the same stage. These anticlinals may intersect either of the primary, or octant, walls, and sometimes, by their early shifting, one may be in doubt as to which wall really separates the octants (*e. g., fig. 78*).

The dermatogen is usually cut off by the second series of walls in each upper octant (*figs. 78, 81*-right, *82*-left). In octants where the first wall was periclinal, differentiating the dermatogen, the second wall is usually an anticlinal, in the inner of the two cells by the first division (*fig. 81*-left). The next walls generally occur as a series of periclinals, giving three concentric layers of cells in the upper octants, as in *fig. 83*. The regularity in this part of the embryo is soon lost, and there arises a mass of parenchymatous tissue in which division may occur in any direction. By repeated anticlinal divisions the dermatogen grows to keep pace with the increase in the bulk of the tissue beneath it.

When each upper octant has undergone its first division, the four lower octants are still undivided (*figs. 76, 77*). The dermatogen is cut off here by the first walls (*figs. 78, 79*). The second division is probably always in the inner cell, thus separating periblem from plerome. *Fig. 79* (left) is not conclusive on this point, but *fig. 84*, in which a series of transverse walls has arisen, shows at the left that periblem and plerome cells arise by the division of an original inner cell. As a result of these divisions three concentric layers of cells are formed in the hypocotyledonary part of the embryo, as is shown in *figs. 80, 81*.

While the primary tissues are thus being differentiated, the cells of the lower octants are becoming considerably elongated (*figs. 78-81*); and soon a series of transverse walls appears, by which two similar tiers or layers of cells are formed, as shown

in *figs. 82–85*. Before this last process is completed, the plerome cells may begin to divide into an inner and an outer layer, as seen in the left lower octant of *fig. 86*. This makes the plerome of this region consist of two concentric layers of cells, a condition shown again in *figs. 89–91*. In *fig. 91*, at the left, the outer of these layers is again splitting in two.

We must now return to the consideration of the cell below the octants, in order to discover what it contributes to the embryo. Starting with the middle cell of *fig. 69*, it is easy to trace it, with the vesicular cell next to it, through *figs. 70–73*, *75* and *76*. This cell, or its product, is labeled *c* throughout the figures. In *fig. 74*, cell *c* has divided once, longitudinally. In *fig. 75*, judging by the size of the cells, *c* is undivided, while the vesicular cell has acquired a transverse wall. In this way a varying number of suspensor cells may arise.

The longitudinal wall in cell *c*, shown in *figs. 74* and *77*, is soon followed by a second one at right angles to the first, giving a tier of four cells, three of whose nuclei are shown in *fig. 79*. In *figs. 78* and *82*, periclinal walls have arisen, cutting off an outer dermatogen layer. It will be seen that cell *c* is undergoing a series of divisions exactly similar to those arising in the lower octants. A second series of periclinal walls, predicted in *fig. 86*, and incomplete in *figs. 83* and *88*, is completed in *fig. 89*. In *figs. 90* and *91*, the innermost of these three concentric layers has split again longitudinally.

The claim of an "addition to the embryo" from the "suspensor" is not a new one. It will be sufficient to cite from two of the more recent papers upon Composite embryology. Mottier (**20**) finds that in *Senecio aureus* the cell below the octants contributes dermatogen and periblem to the embryo, the root cap, to judge by his figures, being organized by the next cell. He makes no specific statement upon this point. Schwere (**24**) finds two "suspensor" cells adding dermatogen and periblem to the embryo of Taraxacum, while the third cell organizes the root cap.

The embryo of Silphium differs from that of Taraxacum in that the product of but one original cell lies between the octants

and the cell organizing the root cap; it differs from Senecio in that this one cell contributes not only dermatogen and periblem, but also the terminal portion of the plerome.

The possibility that the tier of cells called *c*, in embryos older than that in *fig. 77*, arose by the transverse division of the inner octants, has of course presented itself. But in such a case the cells above and below the dividing walls would show clear indications of their being thus related, and the two tiers would be symmetrical as to number and position of cells on either side of the dividing line. Such a symmetry is illustrated in the lower octants of *figs. 82* and *85*, where two tiers of cells are in a process of separation. But no such symmetry is to be found between tier *c* and the tier above it, in any of the figures on *plate V*. These two tiers proceed at very different rates of growth, as a comparison of *figs. 78* and *85* or *86* plainly demonstrates. Moreover, in the study of such a stage as *fig. 79*, the longitudinal walls separating the octants are, we may say, in the plane of the paper and perpendicular to it, respectively; whereas the corresponding walls in tier *c* always run in different planes, being frequently inclined as much as forty-five degrees to the longitudinal walls in the octants. These facts prove conclusively that tier *c* has an origin independent of the octants, and that the description of its ultimate fate, as already given, is correct.

There yet remains for us the consideration of the origin of the root cap. This point seems to have suffered from a general neglect. Hofmeister (1) gives a short description of Helianthus, but no detailed study of the sequence of cell divisions was made.

The first account giving any reliable data upon the point in question is that of Hanstein (2), whose description of the process in Capsella has already been mentioned, and is too familiar to need repetition. In a second mode of cap origin, described for Œnothera, a lenticular cell is cut out from the upper surface of the hypophysis cell, and becomes the periblem terminal; while the remaining portion produces the dermatogen of the root, by the splitting of which the cap arises. Hanstein does not describe any Composite embryos.

Reinke (3) treats of the structure of the root tip in later stages, but not at the time of the first appearance of the cap. He reduces the roots of all phanerogams to one type, that found in Helianthus, with separate initials for plerome, periblem, and dermatogen, the latter proliferating to form the cap.

Fleischer (6) describes a mode of cap origin identical with Hanstein's Capsella, but gives no figures. His account derives the cap from the cell next to the octants, differing in this respect from all other descriptions of Composite embryos. In the structure of the older root tip he agrees with Reinke.

Janczewski (4, 5) confines his attention to older roots, and distinguishes four types of root-tip structure, one of them being the "Helianthus type." He claims, however, that the cap does not arise by the splitting of the dermatogen, but that the inner layer of the root cap is a "calyptrogen," which later abandons its protective function and becomes the epidermis. Later authors have assigned various plants to the "Helianthus type," without noticing that their description agreed with Reinke's account, rather than with that of Janczewski. The validity of the Helianthus type is not to be questioned, for these two views are really but two different interpretations put upon the same structure, Reinke's view having been adopted by all the later writers as the more natural one.

Holle (8) claims that the Helianthus type is the characteristic one for dicotyledons, and that all other types are mere variations. The primary origin of the root cap is not discussed.

In the embryo of *Senecio aureus*, according to Mottier (20), the cell below the octants divides first by one or two transverse walls, and the resulting cells divide longitudinally, adding dermatogen and periblem to the embryo. The cap is probably formed by the next cell below, that is, by the second "suspensor cell."

Maxwell (22), although doing no work upon the Compositae, has given us one of the best reviews, in English, of the work of these earlier writers.

Schwere (24) finds that in Taraxacum the first and second cells of the suspensor add dermatogen and periblem to the

embryo. A third cell divides transversely, its inner half completing the dermatogen and its outer half becoming the first layer of the root cap.

It was seen very early in the course of the investigation that Silphium did not follow the process found in Capsella, and described by Fleischer for Helianthus. Nor could the stages found be made to agree with Schwere's Taraxacum embryos. The mode of origin of periblem and dermatogen terminals resembles more nearly the process as found by Hanstein in Œnothera, the greatest difference being in the origin of the periblem terminal. This, instead of being cut out as a lenticular cell from the upper side of the hypophysis cell, is apparently formed by the intersection of three walls, inclined so as to meet the basal wall of tier *c*. *Figs. 86* and *88* partially illustrate this process. The first of these three walls may at first appear to be longitudinal, as in *fig. 81*, but it is plainly oblique in *fig. 86*. In *fig. 88* the second oblique wall is shown, and a third nucleus, in the tier below the periblem terminal, but in another focus, gives proof of the presence of a third dermatogen terminal.

In *fig. 89* the periblem terminal has divided by probably two longitudinal walls, giving a plate of four cells. In *fig. 90*, by a shifting of the cells, the periblem terminals have been drawn still farther into the pear-shaped body of the embryo. Another wall in the dermatogen terminals gives three cells in section, the middle one being quite broad. In *fig. 91* the two lateral dermatogen terminals have split to produce a layer of the cap; and the presence and direction of the spindle in the middle cell furnishes conclusive proof that the root cap arises by the splitting of the dermatogen. *Fig. 92* shows a portion of a much older embryo, seen entire in *fig. 92, a*. The relations of the primary tissues are the same as in *fig. 91*. The boundaries between plerome and periblem are made heavy, and the epidermal cells are drawn with nuclei. The greater thickness of the cap at the end of the embryo is caused by the splitting of the layers of the cap itself, as can be seen clearly in several places. The apparent diminution in the size of the cells is almost entirely due to the

fact that the magnification of *fig. 92* is but two thirds of that of *fig. 91*.

At this time the cotyledons are nearly half as broad as long, and the tissues of the ovule are reduced to a thin sac, loosely covering the embryo. Ample protection for the growing embryo is provided by the hard walls of the ovary. Older stages of the embryo were not studied, as the increasing hardness of the ovary wall made the rapid fixing of the ovule and embryo more and more difficult.

SUMMARY AND CONCLUSIONS.

In the general features of its development, the foregoing account of the life history of Silphium agrees with those of the other Compositae. But so many facts are peculiar to the genus, that a *résumé* of the course of development is necessary, and a comparison with other Compositae.

The flowers of Silphium in their adult form are of two kinds, the disk flowers being staminate and sterile, the rays being fertile and without stamens.

The order of development of floral organs in the disk flower is corolla, stamens, carpels, calyx. The nectary appears just before the pappus. There is never any trace of ovary or of ovule. The pappus is almost entirely wanting.

The floral organs of the ray flower, in the great majority of cases, appear in the same order as in the disk. The stamens almost always remain as mere papillae, but a few flowers were found in which they had formed pollen mother-cells. The ovary is formed as a cavity between the carpels. The ovule is terminal and cauline, as is shown by its position and bundle relations. This claim is not in accord with the other special accounts for Compositae, but agrees with the claim for a primitive cauline ovule in this family, made recently by Campbell (**30**). Proofs for this claim, however, are first presented in the present paper.

In that the hypodermal archesporial cell develops a row of four potential megaspores, of which the inner one germinates to form the embryo sac, Silphium resembles all the other

Compositae which have been described. Eight chromosomes were counted in the megaspore mother cell. The number has not been reported for any other genus.

Four of the five species studied — *S. integrifolium*, *S. trifoliatum*, *S. terebinthinaceum*, and *S. laciniatum* — resemble each other in the general structure of the embryo sac. The synergids and oosphere are somewhat pear-shaped, the egg being inserted near the apex of the sac. The polar nuclei fuse before fertilization, and the definitive nucleus lies near the egg apparatus. The antipodal cells are arranged in a row, and, as is common among Compositae, tend to increase in number beyond the original three. The growing sac quickly ruptures the nucellus, and the basal portion of the latter is to be found as a remnant by the side of the antipodal cells. The terminal portion generally remains perched on the apex of the sac, forming a densely staining cap. In one case these nucellar cells had continued their growth in this position. Such a nucellar cap is new for Compositae, but has been reported in various aroids by Campbell (**30**) and others.

The embryo sac of *S. perfoliatum* is like that of the other species in most respects, but presents a very different appearance in its micropylar portion. There is no nucellar cap. The synergids are very much elongated, their tips being filled with a very dense protoplasm. They do not, however, rupture the tip of the sac.

The development of the microsporangia follows the well-known order, the steps of which need not be repeated. By the failure of the last series of divisions, the middle layer may be lacking, the sister layer to the tapetum in this case developing into the endothecium. The sporogenous cells divide at least once after the tapetum begins to take a differential stain.

The nuclei of the pollen-mother cells show a well-marked synapsis stage, and pass quickly from this to the formation of the spindles for the first division. In the equatorial plate of this spindle the reduced number of chromosomes, eight, was repeatedly counted. The second division follows immediately after the first.

The division of the nucleus of the pollen grain into a vegetative and a generative nucleus, and the division of the latter into two sexual nuclei, apparently follows the usual order. The male cells are at first round, but in three of the five species examined they become greatly elongated, often acquiring a remarkably spermatozoid-like form. Such a form of male cells has been reported among various monocotyledons, but up to the present time Silphium is the only dicotyledon reported as showing them.

The pollen tube enters the embryo sac just beyond the edge of the nucellar cap. Fertilization may be accomplished without the previous disorganization of either of the synergids. The division of the definitive nucleus precedes the division of the oospore.

The first wall in the oospore is, as usual, transverse. It is possible, though not certain, that, unlike the other Compositae described, the terminal cell of the two-celled stage divides again transversely, and that the real "embryo cell" is the outer cell arising by this second division.

The first wall in the embryo cell is a radial longitudinal one, instead of being transverse, as is said to be the rule for Compositae. The second or quadrant wall is likewise almost always longitudinal, and separates the two cotyledons. The transverse walls separating the octants are the third series to appear.

The first series of walls in the outer octants is oblique, the dermatogen being cut off by the second series. In the inner octants the first walls differentiate the dermatogen, and the inner cells divide again to produce the periblem and plerome.

The cell below the octants, cell *c*, by divisions exactly similar to those in the inner octants, forms a tier of cells which adds to all the primary tissues of the embryo.

The periblem terminal is formed by the intersection of three oblique walls in the cell next below cell *c*. The other daughter cells in contact with the periblem, terminal complete the dermatogen of the root, and by splitting form the first layer of the root cap.

The relations of the primary tissues remain unchanged in older embryos. Dermatogen, periblem, and plerome have separate initials, and the root cap arises by proliferation of the dermatogen. Thus the embryo of Silphium conforms to the "Helianthus type," as described by Reinke.

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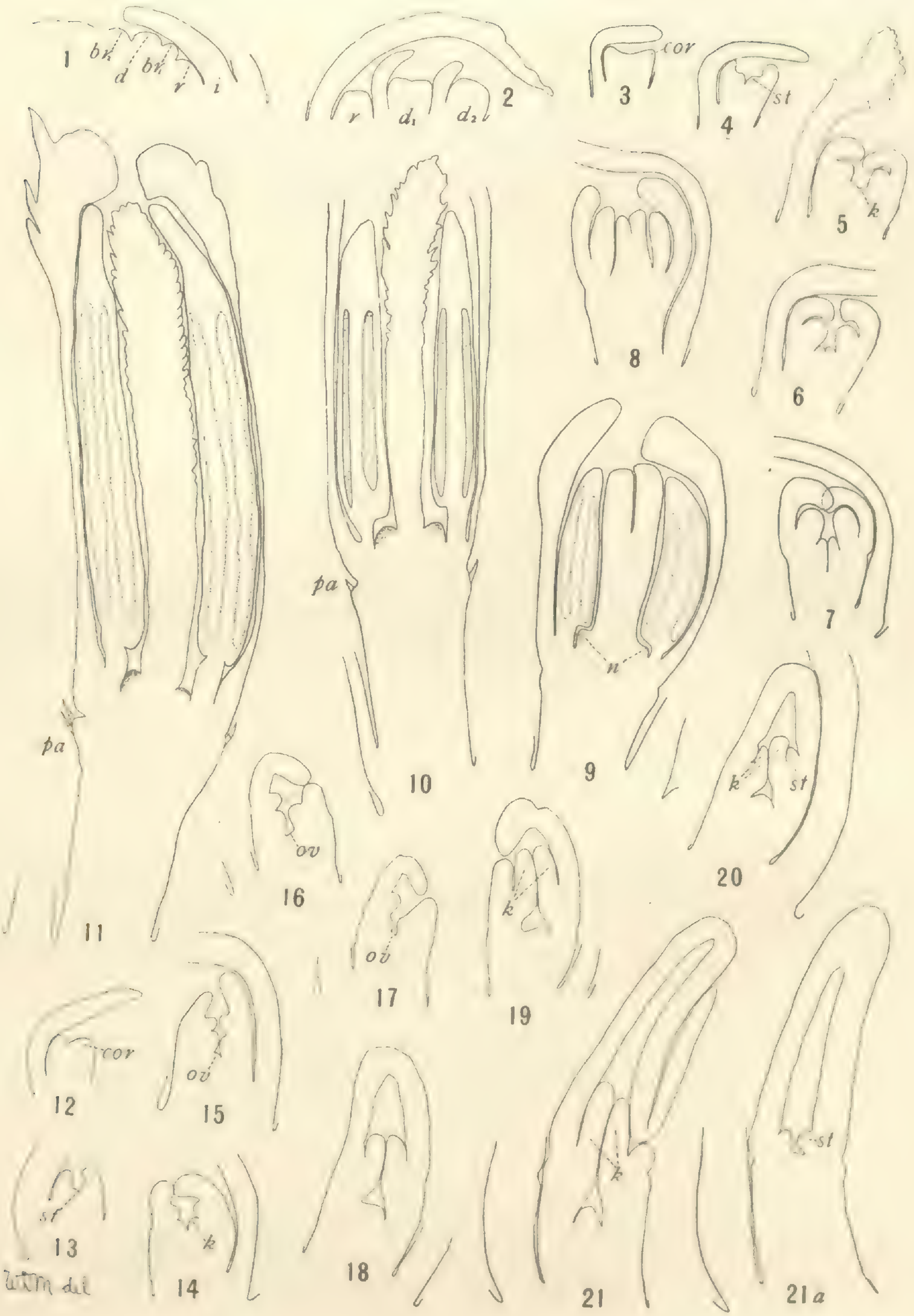
EXPLANATION OF PLATES III–X.

All the drawings were made with a camera lucida. *Figs. 1–27* and *66* were drawn with a Reichert ocular no. 4 and objective no. 3; *figs. 59–63* with Reichert ocular 12 and Bausch and Lomb $\frac{1}{12}$ immersion objective; *fig. 92* with Reichert ocular 2 and Bausch and Lomb $\frac{1}{12}$ immersion objective; all other figures with Reichert ocular 4 and Bausch and Lomb $\frac{1}{12}$ immersion objective. The original magnification will be specified for each figure. The plates are reduced to three eighths of the original size.



MERRELL on SILPHIUM

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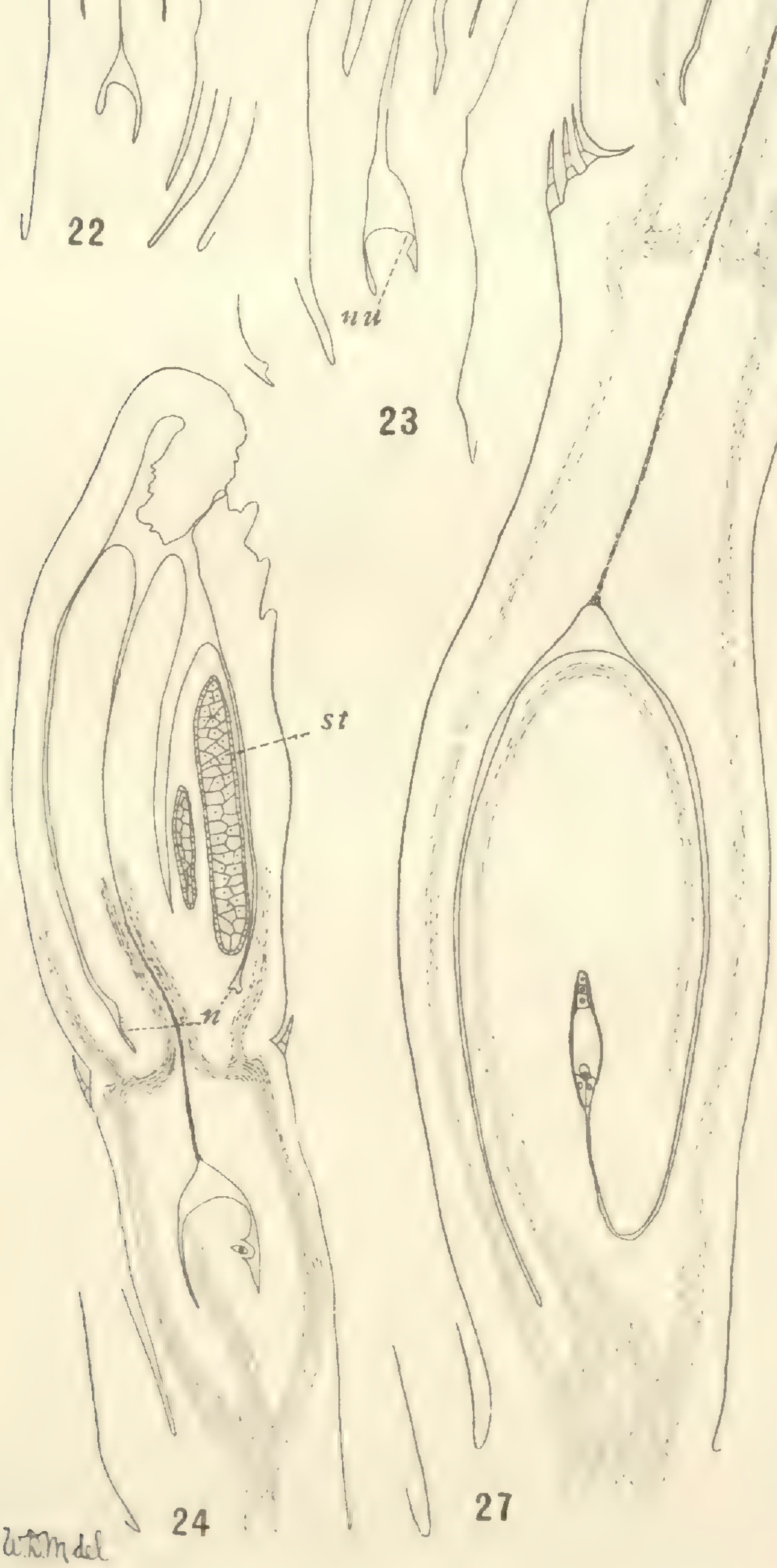

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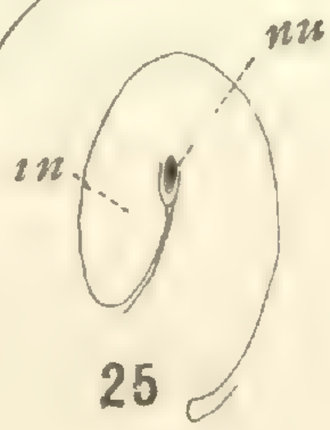

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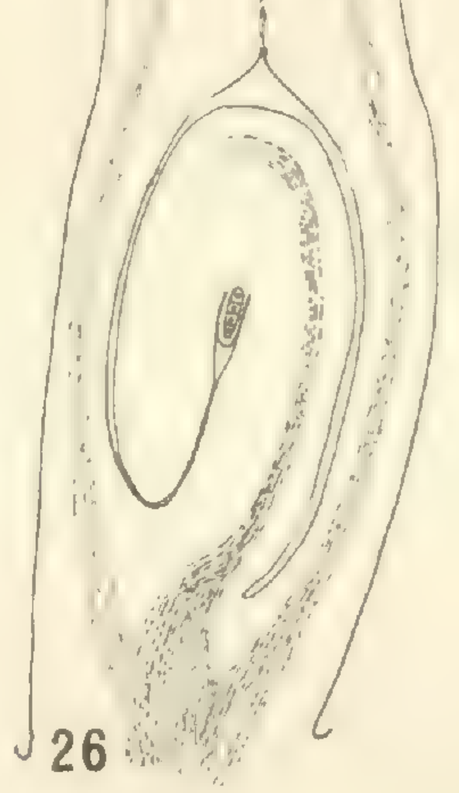

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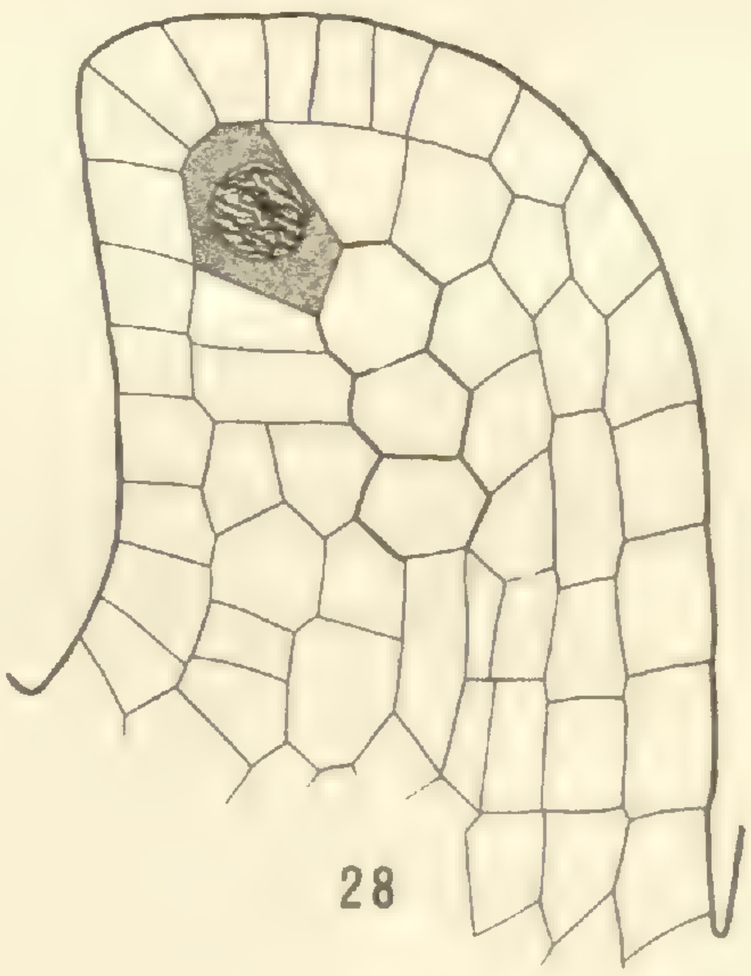

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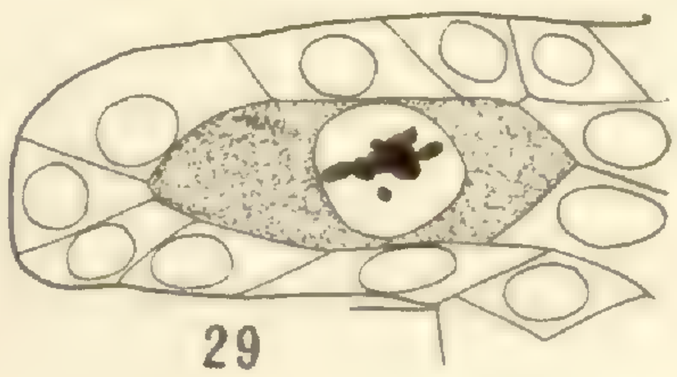

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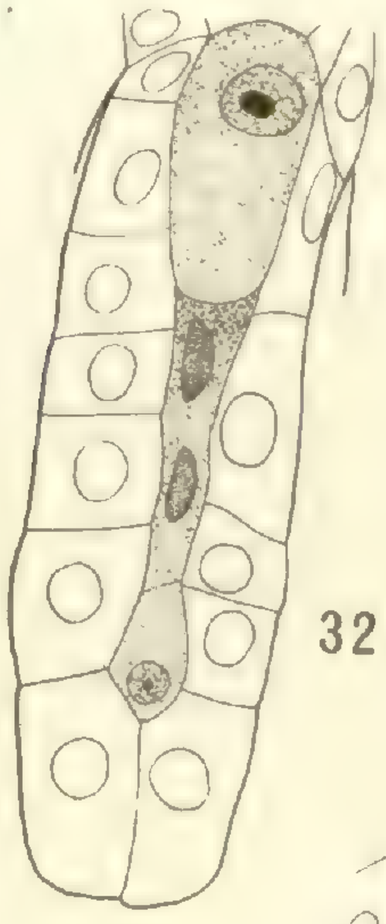

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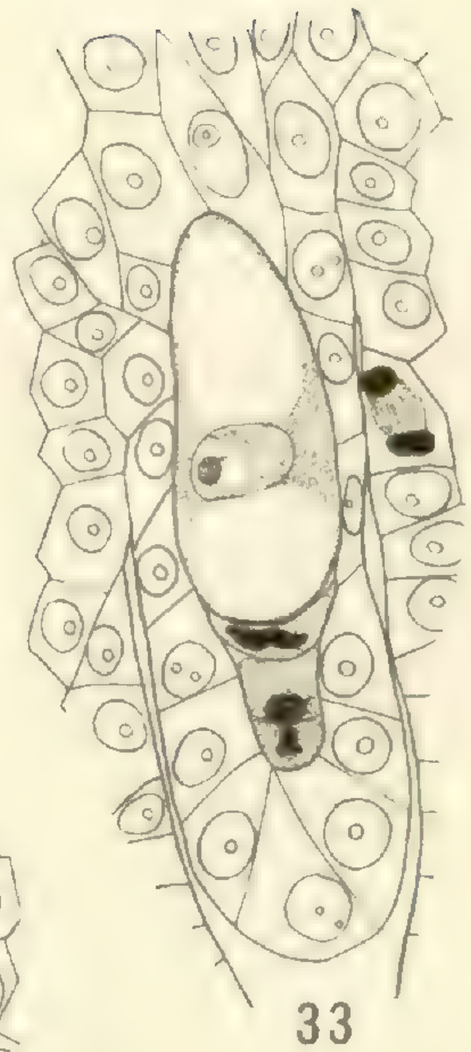

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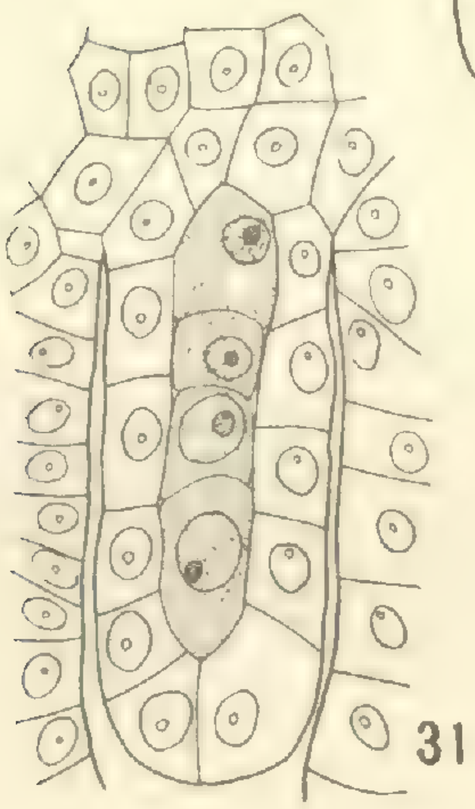

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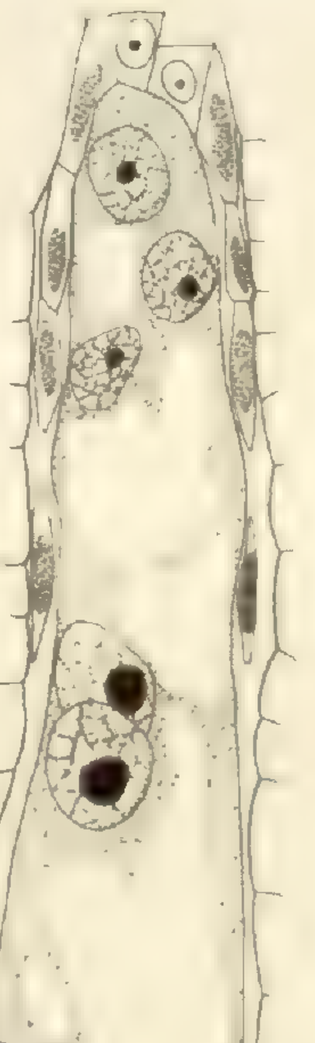

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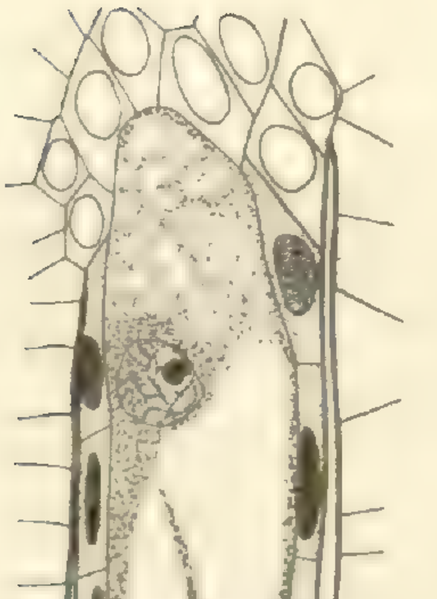

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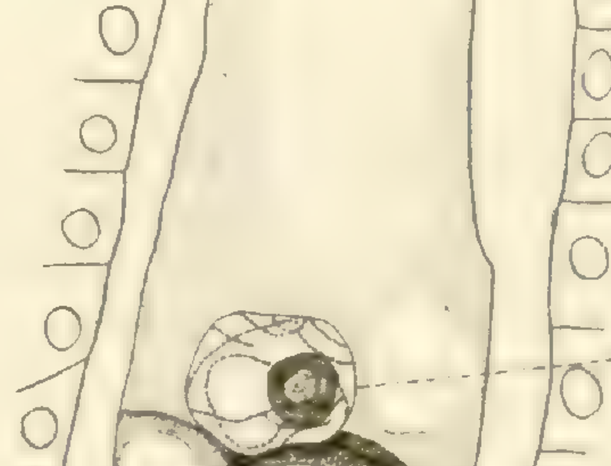

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MERRELL on SILPHIUM

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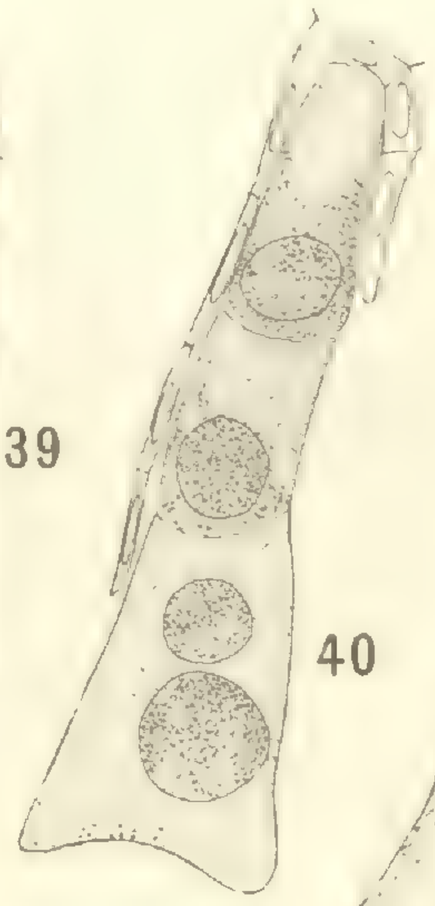

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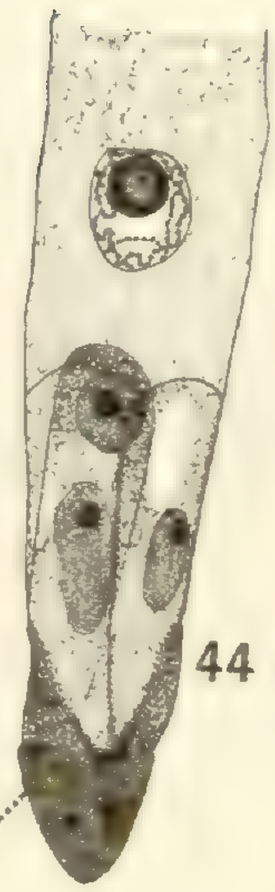

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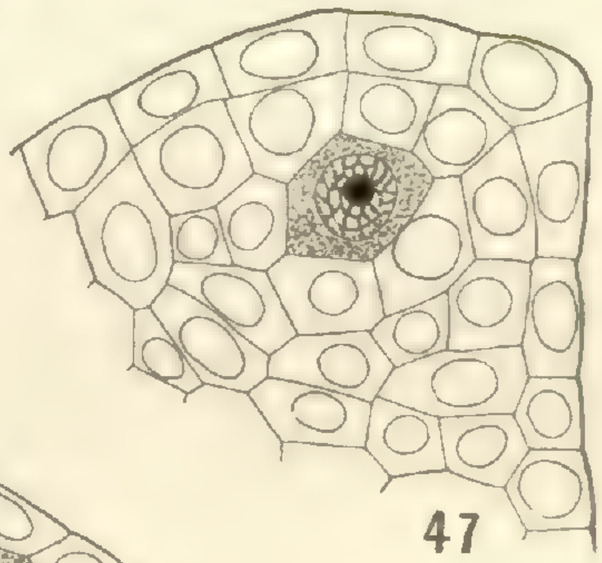

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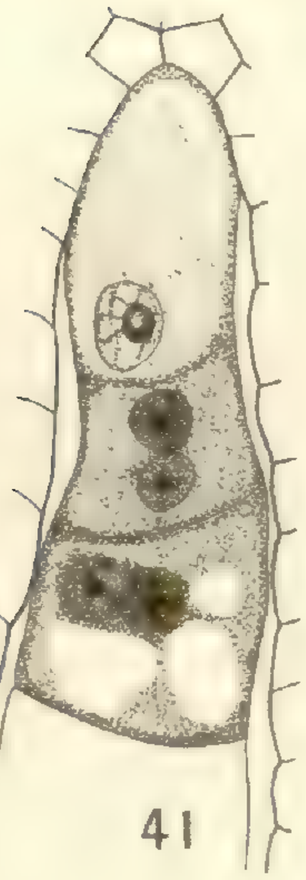

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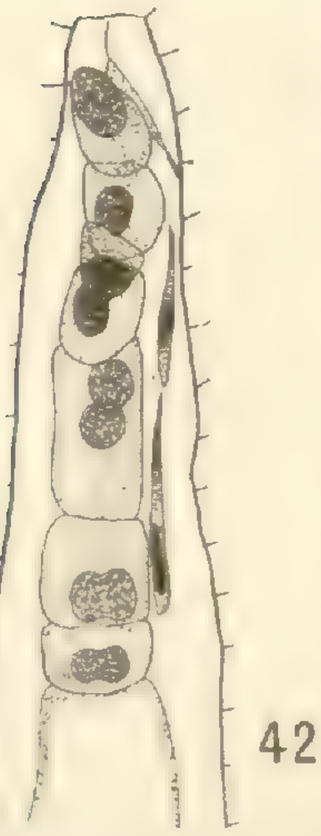

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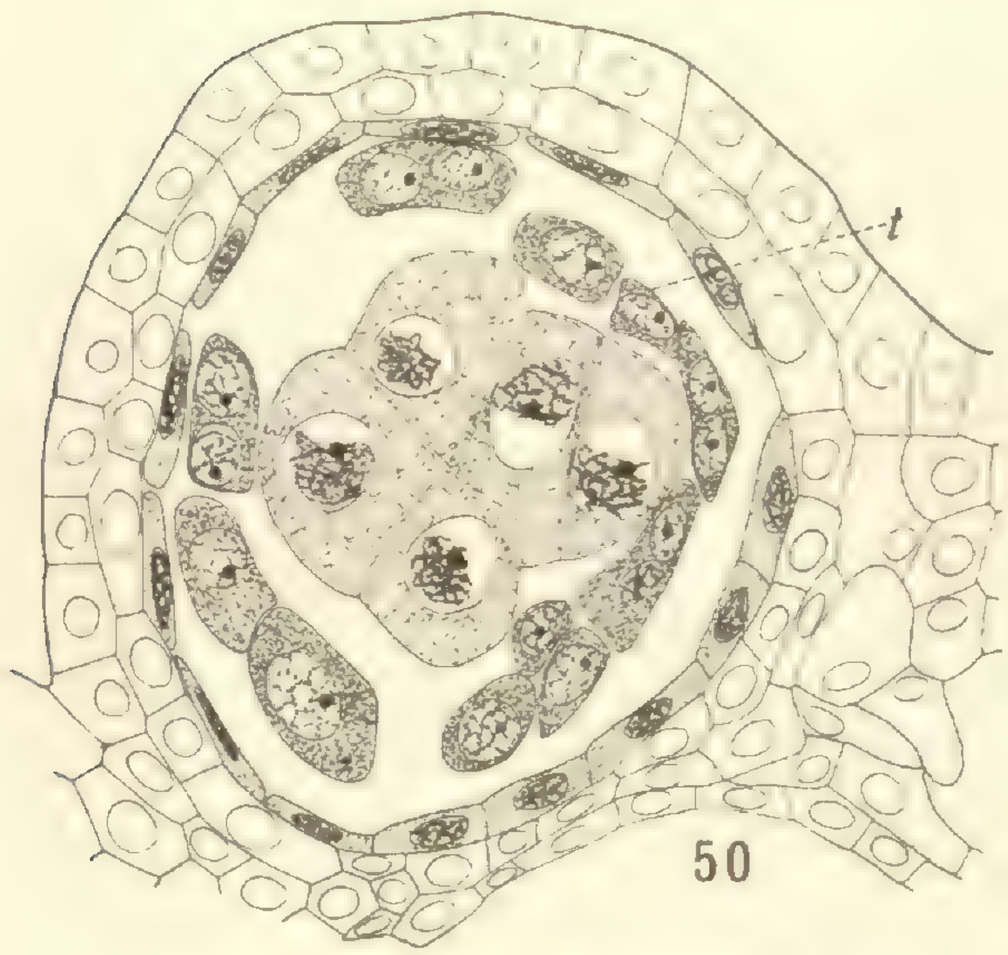
MERRELL on SILPHIUM



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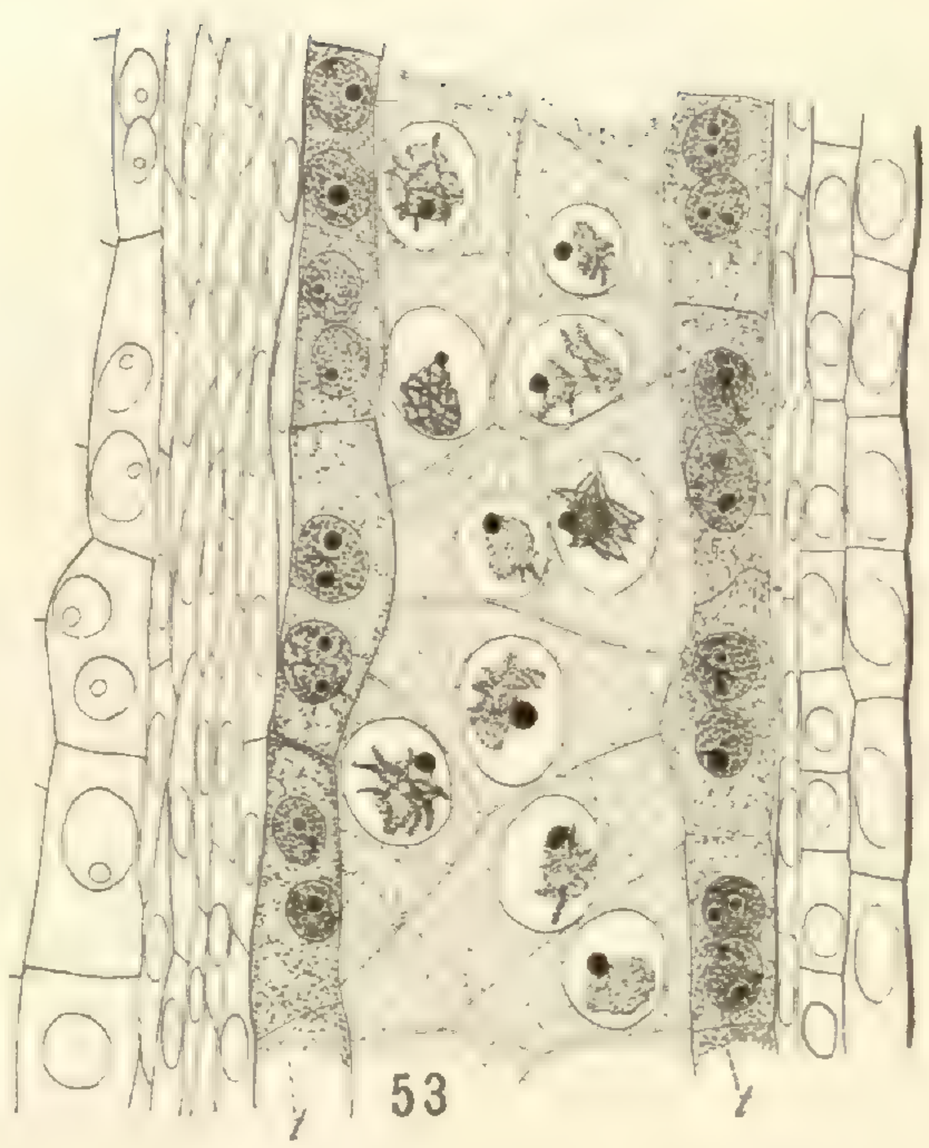

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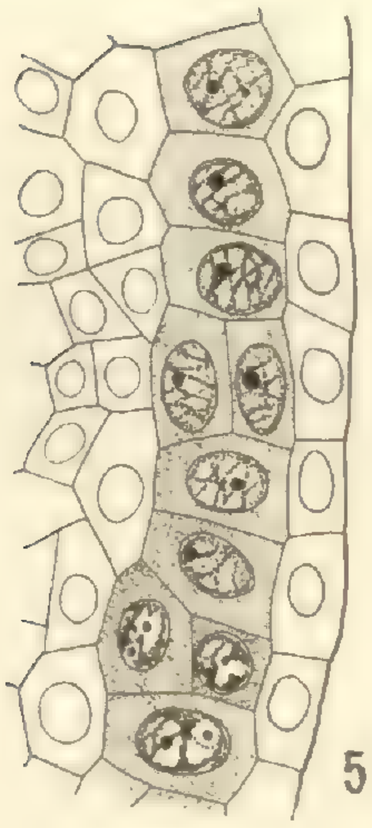

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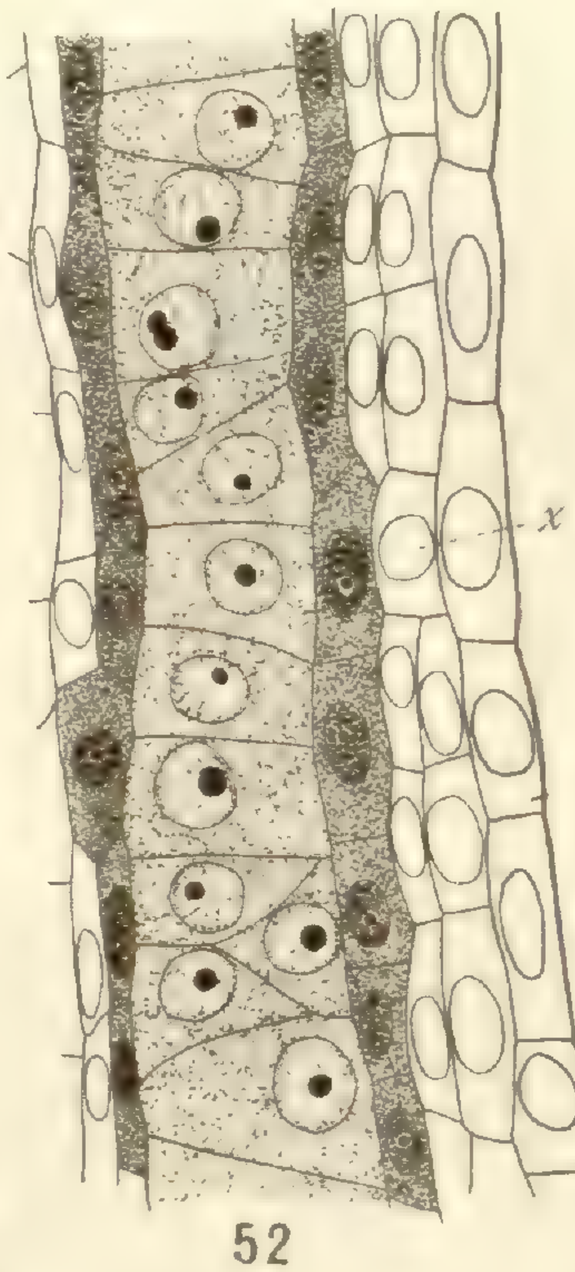

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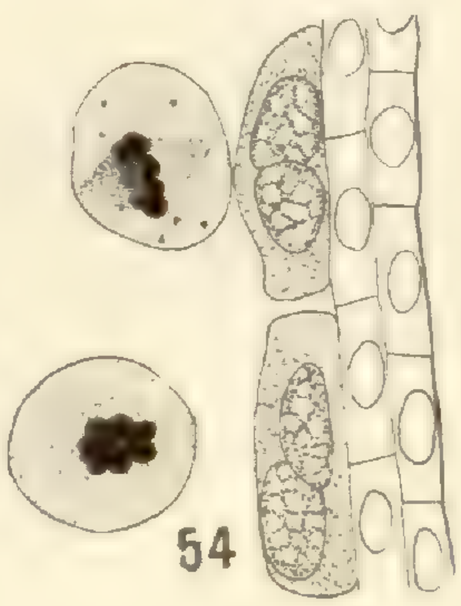

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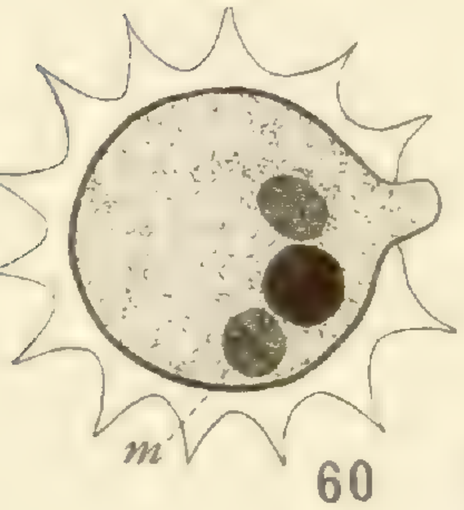

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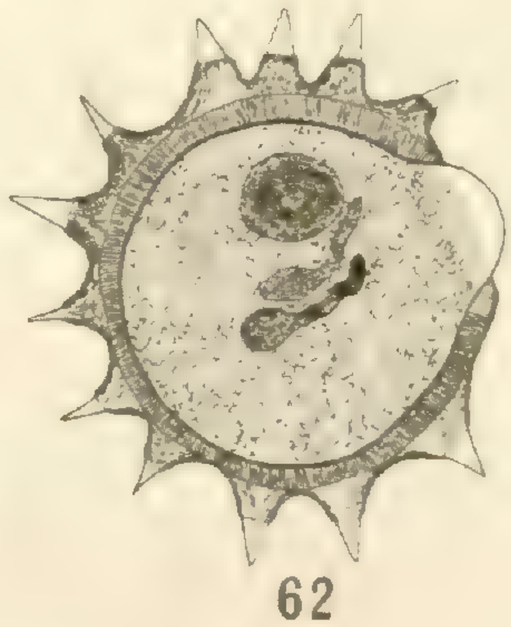

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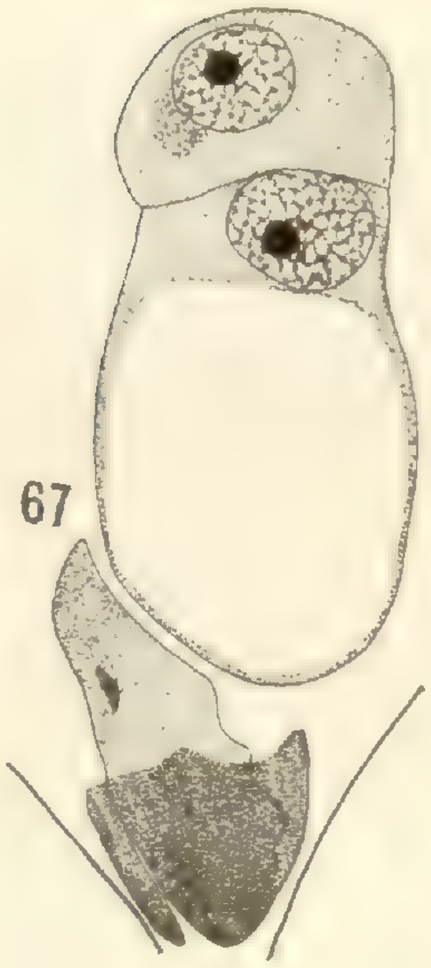

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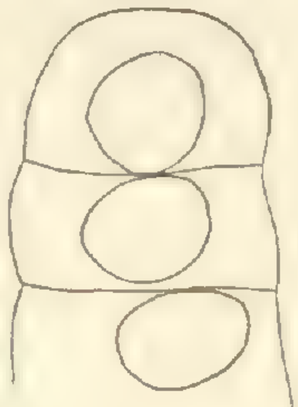

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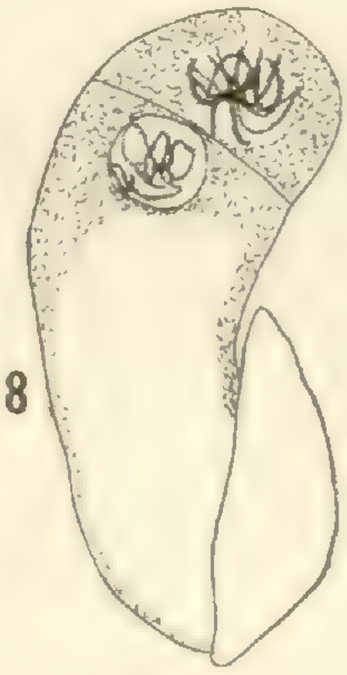

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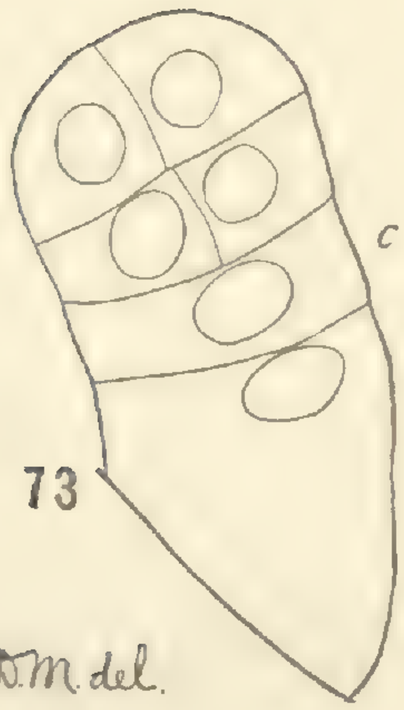

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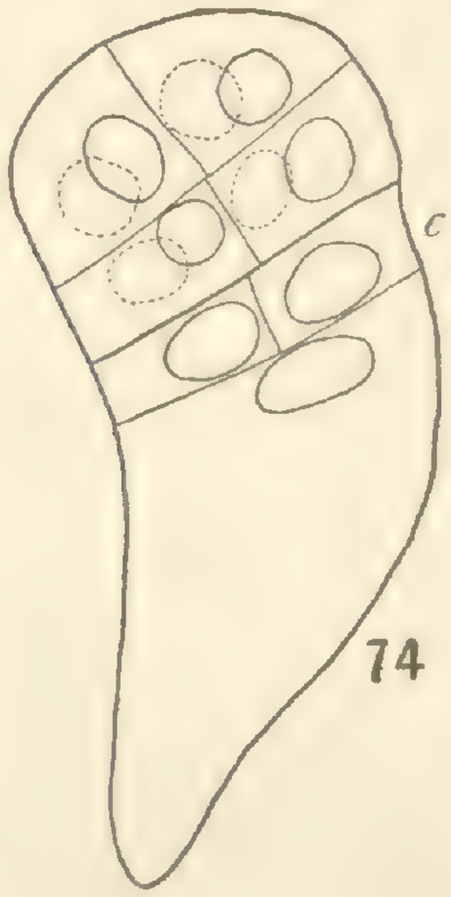

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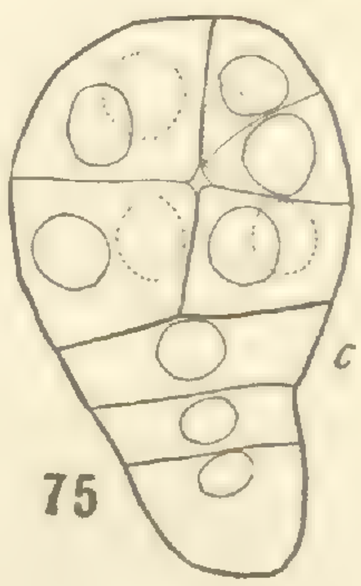

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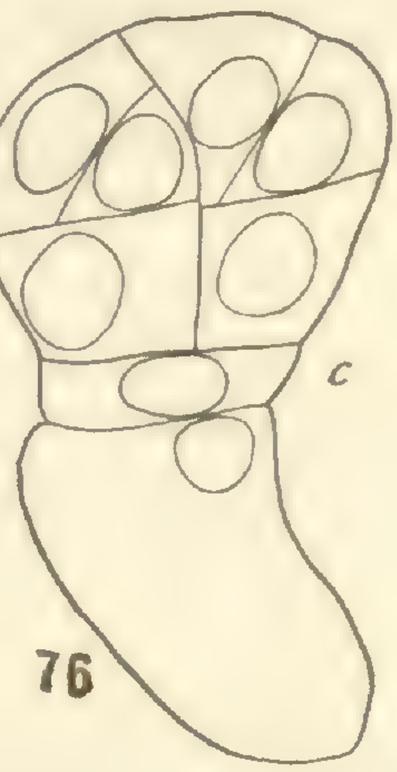

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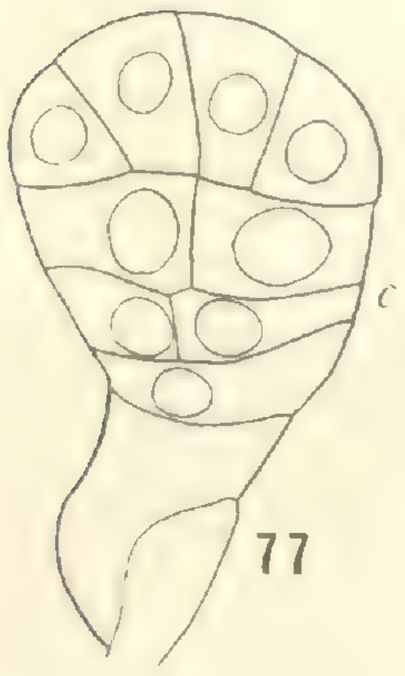

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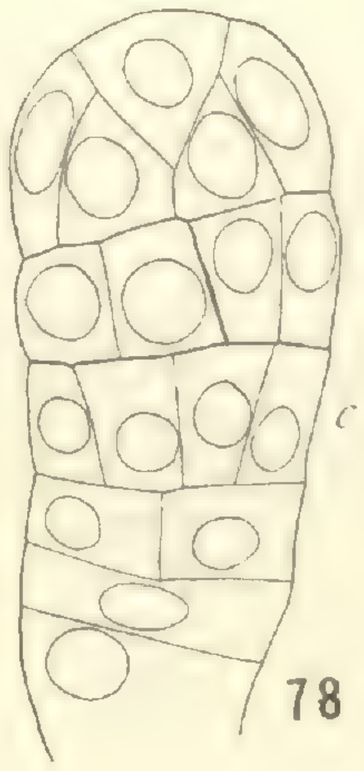

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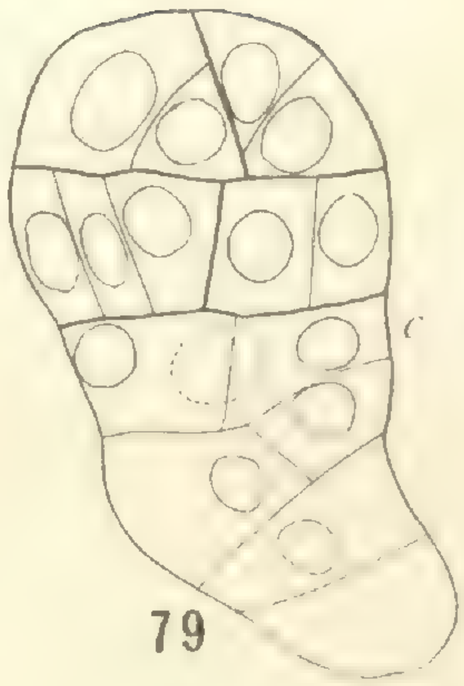

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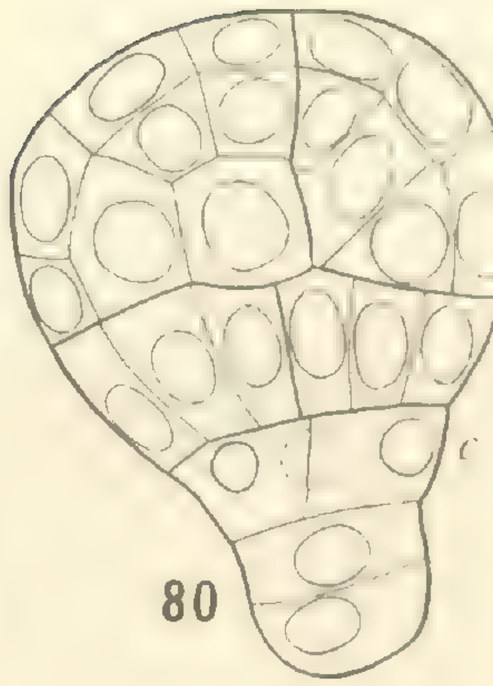

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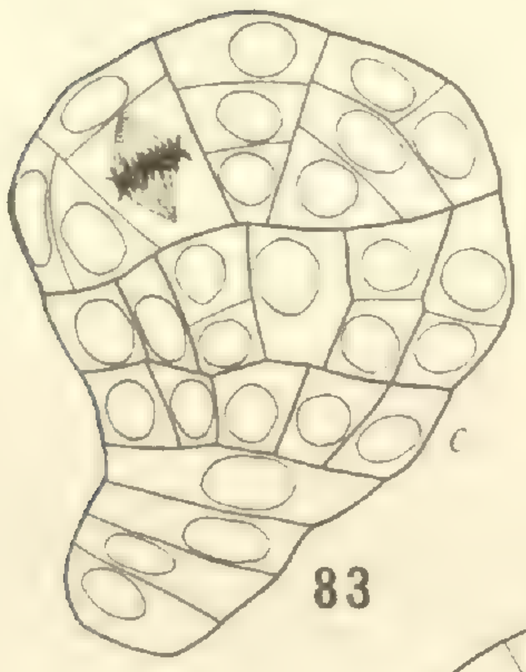

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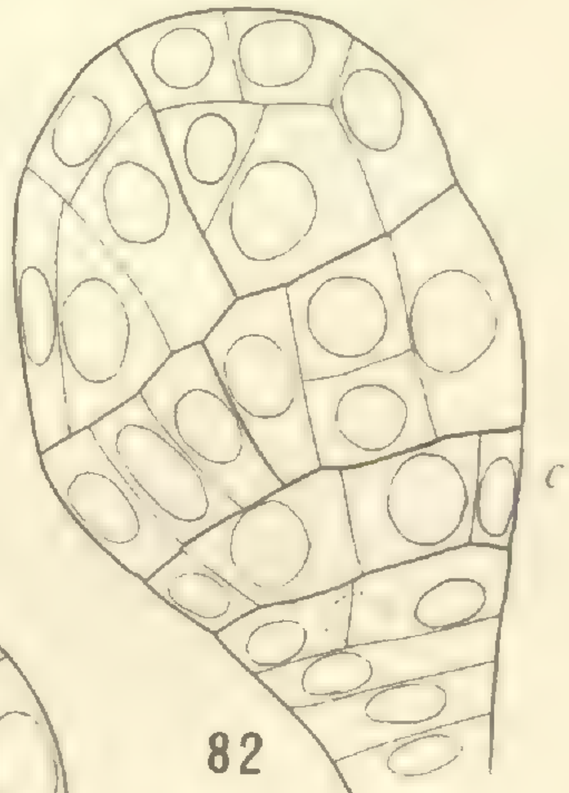

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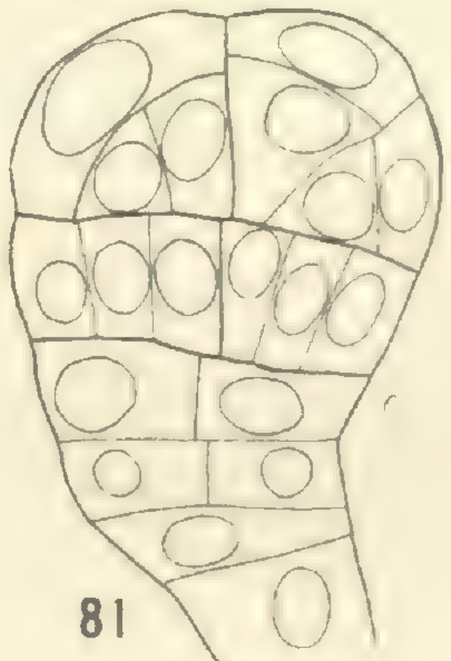

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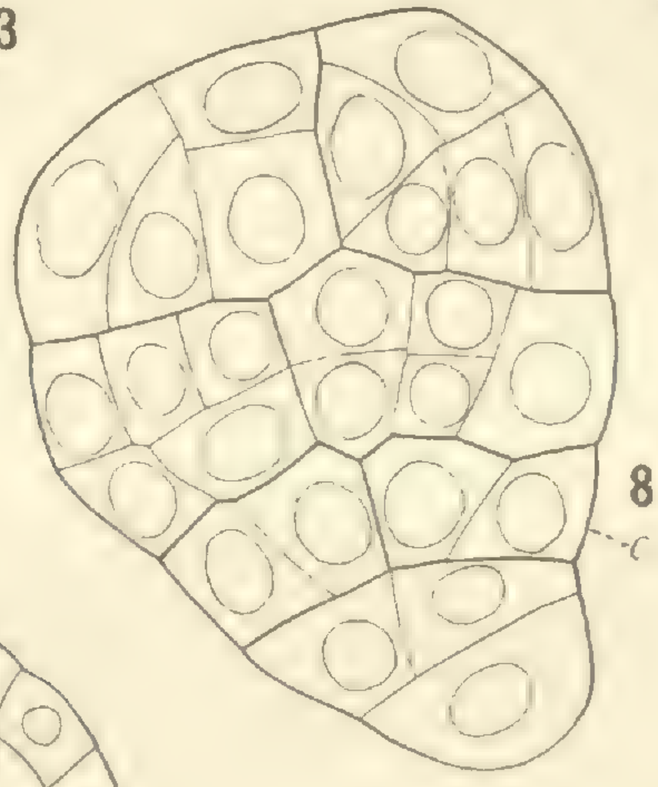

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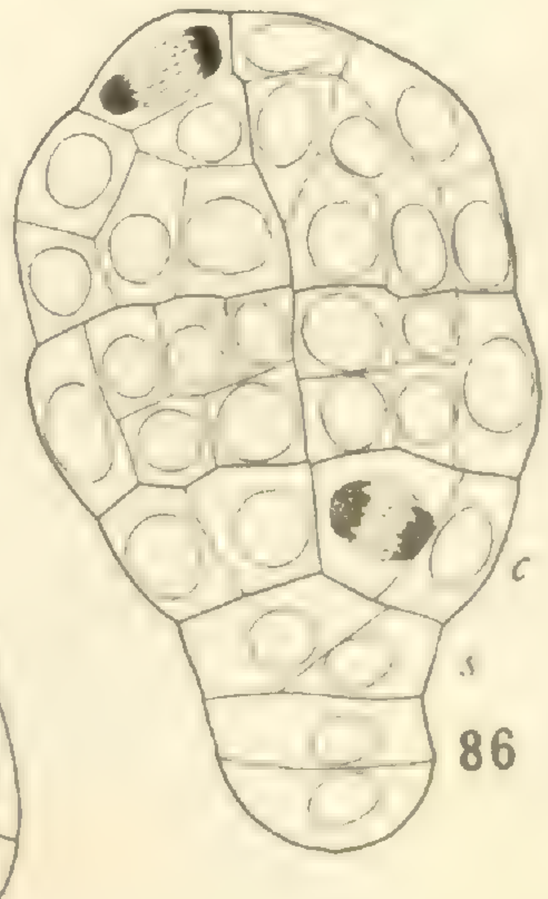

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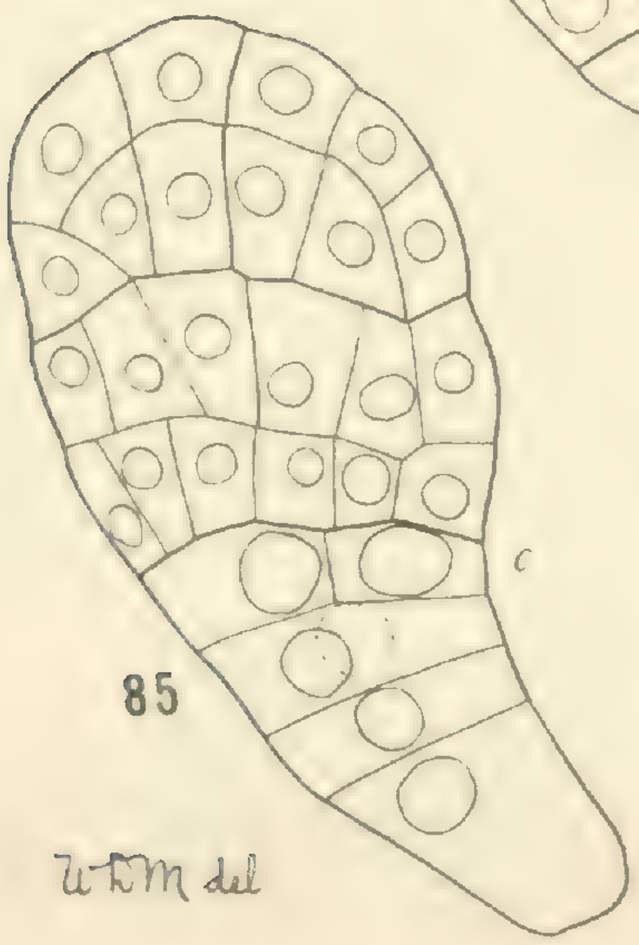

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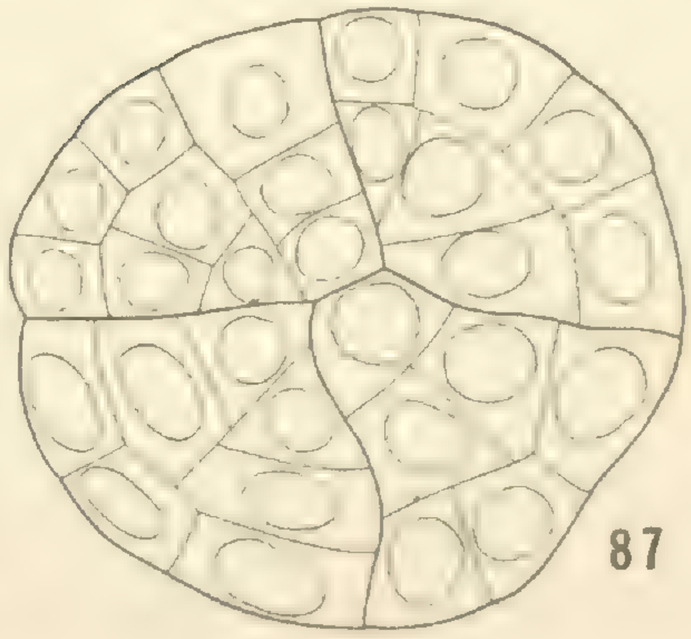

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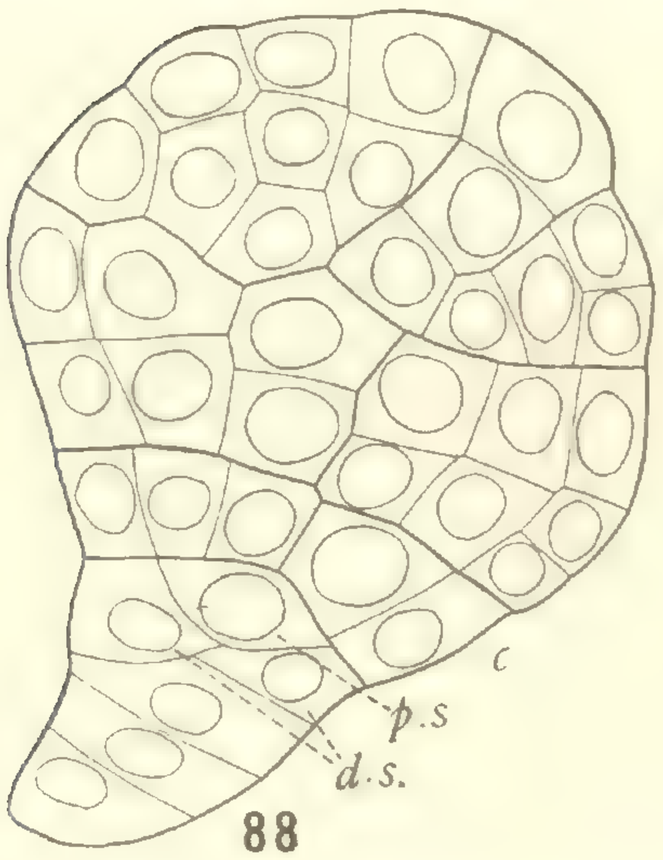
MERRELL on SILPHIUM



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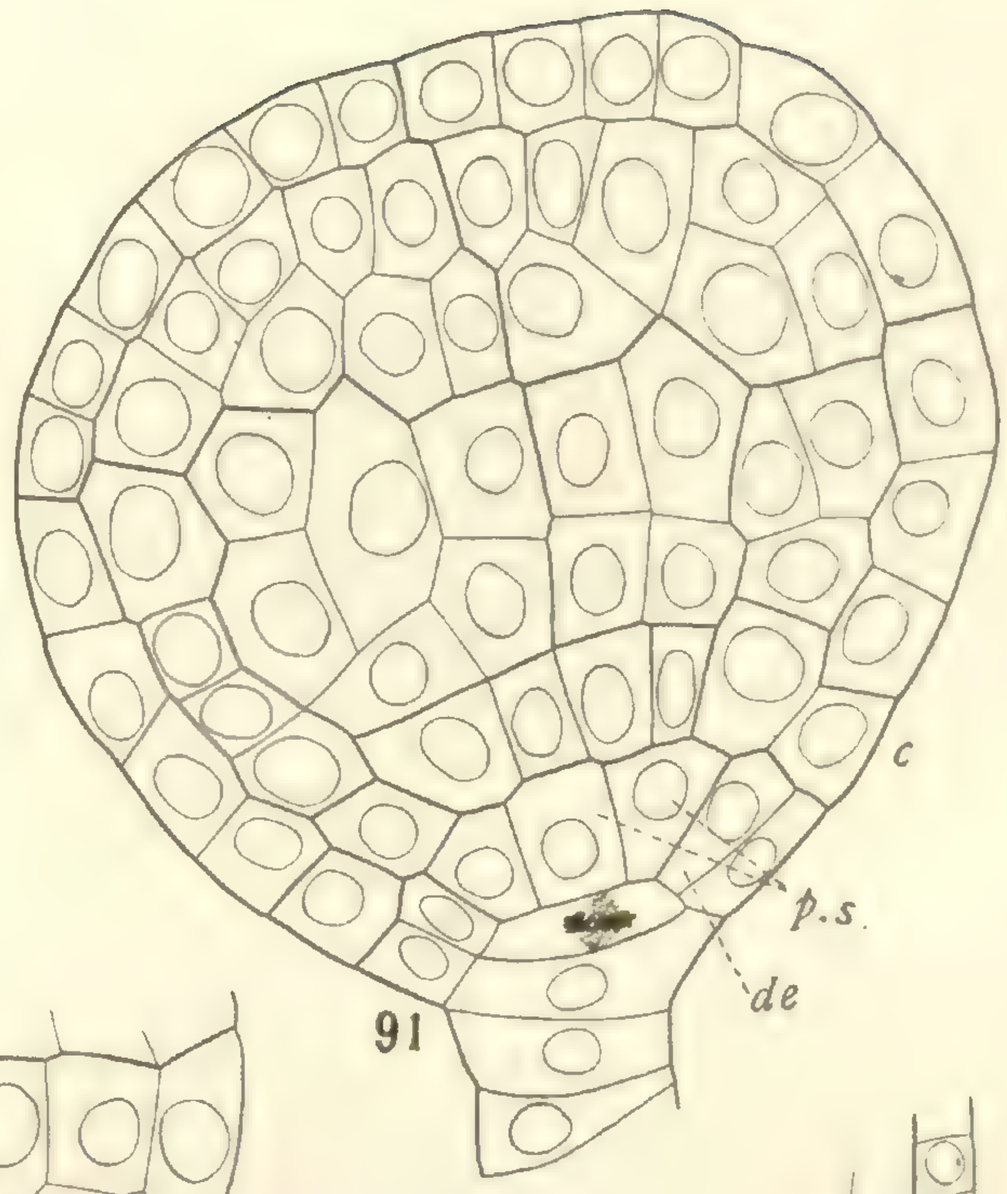

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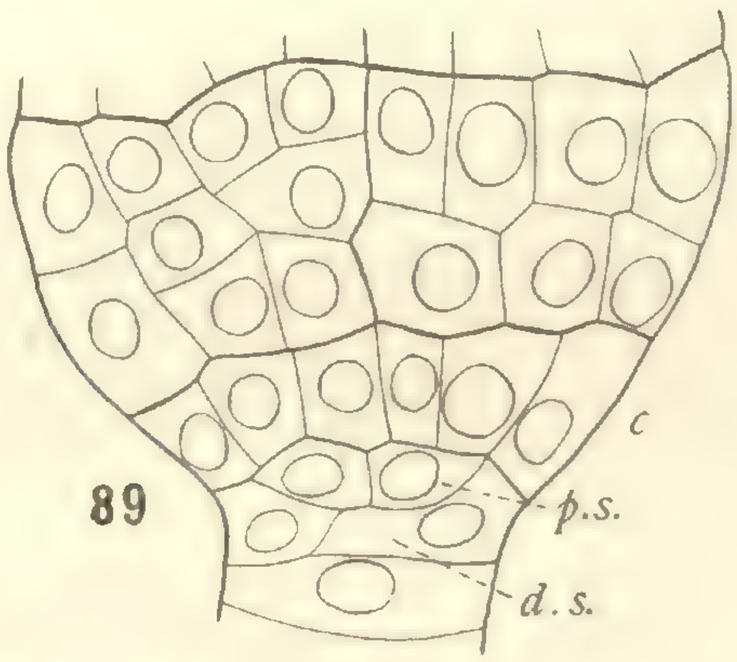

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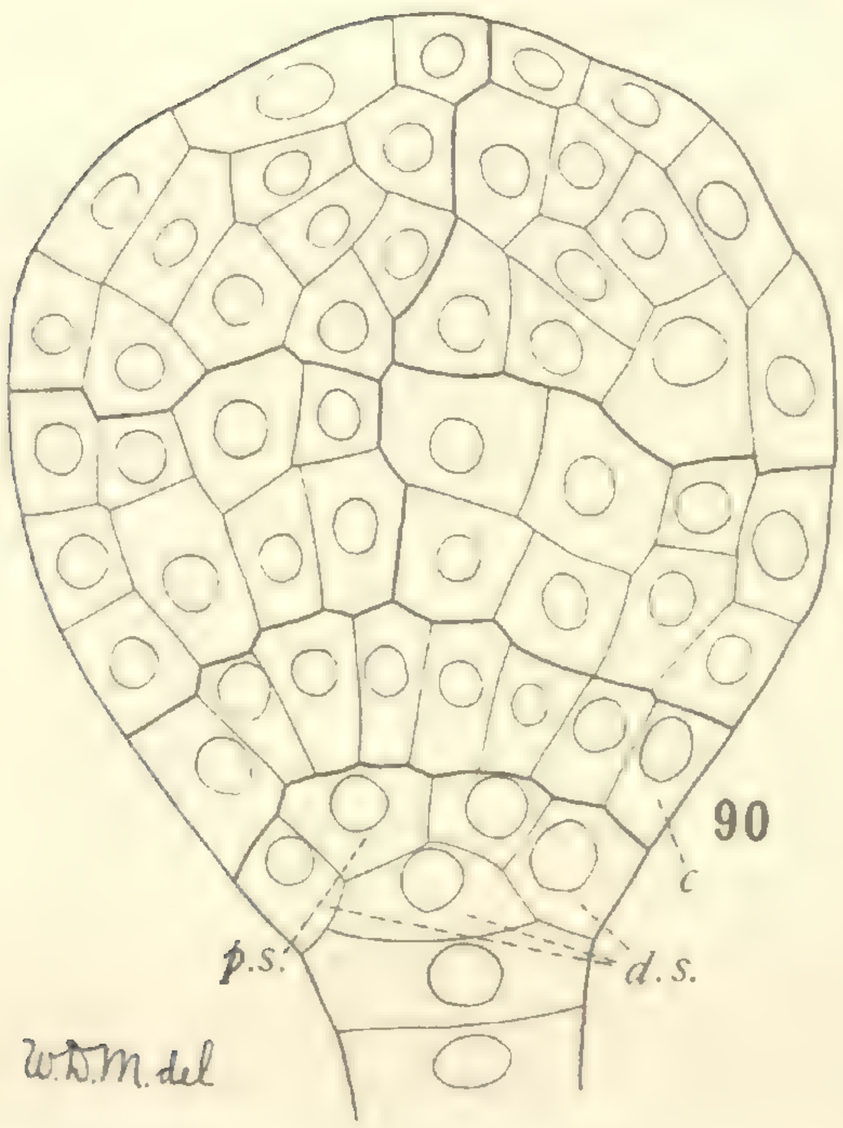

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MERRELL on SILPHIUM

PLATE III

All figures magnified 130 diameters.

FIG. 1. First appearance of individual florets: *d*, disk floret; *r*, ray floret; br_1, br_2, bracts on receptable; *i*, involucral bract.

FIG. 2. A later stage: parts lettered as in *fig. 1*.

FIGS. 3–11. Successive stages in development of disk floret: each part lettered on its first appearance: *cor*, corolla tube; *st*, stamens; *k*, carpels; *n*, nectaries; *pa*, pappus.

FIGS. 12–21. Stages in development of ray floret: *cor*, corolla tube; *st*, stamens; *k*, carpels; *ov*, ovule; the base of the subtending bract indicates the anterior side of the floret.

FIG. 21, *a*. Lateral section of floret whose median section is shown in *fig. 21*: *st*, rudimentary stamens.

PLATE IV

Figs. 22–27, magnified 130 diameters; *figs. 28, 29*, magnified 1375 diameters.

FIG. 22. *S. integrifolium*. Ray floret when archesporial cell first becomes recognizable in ovule.

FIG. 23. Ray floret: nucellus (*nu*) just appearing.

FIG. 24. *S. integrifolium*. Older ray floret, ovule half turned: *st*, half developed stamen; *n*, nectary; course of vascular bundles shown by dotted lines.

FIG. 25. *S. integrifolium*. Ovule at time of first division in archesporial cell: *nu*, nucellus; *in*, integument.

FIG. 26. *S. integrifolium*. Ovary of older floret, showing nectary, rudimentary pappus, ovule, and course of vascular bundles.

FIG. 27. *S. integrifolium*. Ovary and ovule at time of maturity of embryo sac.

FIG. 28. *S. integrifolium*. Details of ovule outlined in *fig. 22*, showing archesporial cell. (Safranin-gentian-violet.)

FIG. 29. *S. integrifolium*. Nucellus of older ovule; nucleus of archesporial cell with one nucleolus and eight chromosomes. (Cyanin-erythrosin.)

PLATE V

All figures magnified 1375 diameters.

FIG. 30. *S. perfoliatum*. Spindle fully formed in archesporial cell; chromosomes in equatorial plate. (Iron-alum-haematoxylin.)

FIG. 31. *S. integrifolium*. Nucellus with row of four potential megaspores. (Saf.-gen.-violet.)

FIGS. 32, 33. *S. integrifolium*. Growth of fertile megaspore and its encroachment upon the sterile cells. (Saf.-gen.-violet.)

FIGS. 34, 35. *S. integrifolium.* Embryo sac with two nuclei. (Cyanin-erythrosin.)

FIG. 36. *S. integrifolium.* Embryo sac with four nuclei; nucellus ruptured. (Saf.-gen.-violet.)

FIG. 37. *S. integrifolium.* Embryo sac with fusing polar nuclei. (Cyanin-erythrosin.)

FIG. 38. *S. integrifolium.* Mature embryo sac: *ca*, nucellar cap; *sy*, synergidae; *o*, oosphere; *en*, primary endosperm nucleus; *an*, antipodal cells. (Saf.-gen.-violet.)

PLATE VI

All figures magnified 1375 diameters.

FIG. 39. *S. trifoliatum.* Two antipodal cells; indications of direct nuclear divisions.

FIG. 40. *S. laciniatum.* Three antipodal cells, the inner one with two nuclei.

FIG. 41. *S. integrifolium.* Three antipodal cells, with a total of five nuclei.

FIG. 42. *S. integrifolium.* Seven antipodal cells, with a total of eight nuclei; ndications of amitotic division.

FIG. 43. *S. integrifolium.* Micropylar portion of embryo sac, showing a nucellar cap (*ca*) whose cells have continued growth.

FIG. 44. *S. integrifolium.* Egg apparatus with nucellar cap, the latter showing remains of cell walls and nuclei.

FIG. 45. *S. perfoliatum.* Mature embryo sac, showing, especially, the long pear-shaped synergidae. (Iron-alum-haematoxylin.)

FIGS. 46–49. *S. trifoliatum.* Portions of transverse sections of young anthers, showing stages in the development of the sporogenous cells and their surrounding layers from the hypodermal archesporium; at *x*, *fig. 49*, the endothecium and middle layer are seen to have a common origin. (Fuchsin-iodine-green.)

PLATE VII

Figs. 50–58, magnified 1375 diameters; *figs. 59–63*, magnified 2400 diameters.

FIG. 50. *S. trifoliatum.* Transverse section of older anther; nuclei of pollen mother-cells in synapsis stage; tapetal cells (*t*) mostly with two nuclei; cells of middle layer also granular and deeply stained. (Fuchsin-iodine-green.)

FIGS. 51–53. *S. integrifolium.* A series of longitudinal sections of anthers, for comparison with the transverse sections. (Cyanin-erythrosin.)

FIG. 54. *S. integrifolium.* Two pollen mother-cells with spindles of the first division, one seen from the side, the other from the end; eight chromosomes; tapetal cells, with two nuclei, lying next to the endothecium; no middle layer. (Saf.-gen.-violet.)

FIG. 55. *S. integrifolium.* Second division inpollen mother-cell. (Iron-alum-haematoxylin.)

FIG. 56. *S. integrifolium.* Tetrad. (Saf.-gen.-violet.)

FIG. 57. *S. integrifolium.* Young pollen grain. (Saf.-gen.-violet.)

FIG. 58. *S. integrifolium.* Older pollen grain, with large vacuole and growing spines. (Cyanin-erythrosin.)

FIG. 59. *S. integrifolium.* Pollen grain with vegetative (*v*) and generative (*g*) nuclei. (Iron-alum-haematoxylin.)

FIG. 60. *S. integrifolium.* Generative nucleus has divided into two male nuclei (*m*). (Saf.-gen.-violet.)

FIG. 61, *a–c. S. integrifolium.* Stages in development of spiral male cells. (Saf.-gen.-violet.)

FIG. 61, *f. S. perfoliatum.* Elongated male cell, showing fine nuclear network and delicate film of cytoplasm. (Iron-alum-haematoxylin.)

FIG. 62. *S. integrifolium.* Pollen grain in detail, showing vegetative nucleus, two male cells, prismatic structure of exine, and the "sheath" derived from the tapetum. (Iron-alum-haematoxylin.)

FIG. 63. *S. terebinthinaceum.* Pollen grain, similar to the last; details of exine and sheath not drawn. (Iron-alum-haematoxylin.)

PLATE VIII

Fig. 66 magnified 130 diameters; all other figures, 1375 diameters.

FIG. 64. *S. laciniatum.* Fertilization; pollen tube (*p. t.*) passing outside the nucellar cap; male nucleus within the oosphere. (Fuchsin-iodin-green.)

FIG. 65. *S. integrifolium.* Dividing primary endosperm nucleus near tip of oospore; cap (*ca*) still perched on end of embryo-sac. (Saf.-gen.-violet.)

FIG. 66. *S integrifolium.* Diagram of sac, showing two-celled embryo and five spindles in endosperm; the synergid (*sy*) might be mistaken for a pollen tube.

FIG. 67. *S. integrifolium.* First division in oospore; synergid and nucellar cap.

FIG. 68. *S. terebinthinaceum.* Two-celled embryo; nuclei preparing for next division.

FIG. 69. *S. integrifolium.* Embryo with three cells, probably by division of vesicular cell of *fig. 68*: *c*, in all figures, designates the cell below the octants, or its product.

FIG. 70. *S. terebinthinaceum.* First longitudinal wall in embryo cell, in radial plane.

FIG. 71. *S. integrifolium.* Similar embryo, side view.

FIG. 72. *S. terebinthinaceum.* Quadrant stage in embryo cell, by two longitudinal divisions.

FIG. 73. *S. integrifolium.* Quadrant stage, by longitudinal and a transverse division.

FIG. 74. *S. integrifolium.* Octant stage; cell *c* with one longitudinal wall.

In each of the above figures the entire embryo has been drawn. The succeeding figures represent median sections.

FIG. 75. *S. integrifolium.* One octant divided by anticlinal wall; three cells in suspensor, by transverse division of vesicular cell of *fig. 73*.

FIG. 76. *S. integrifolium.* Dermatogen cut off by periclinal in one octant, anticlinal wall in other upper octant; two remaining upper octants, not drawn, are like the latter.

PLATE IX

All figures magnified 1375 diameters. *Fig. 82, S. terebinthinaceum;* other figures, *S. integrifolium.*

FIG. 77. Anticlinal walls in upper octants; lower octants undivided; longitudinal wall in *c*.

FIG. 78. Second division, periclinal, in one upper octant; dermatogen cut off in lower octants, also in cell *c*; intersecting walls in cell below *c*.

FIG. 79. Periblem and plerome separated in left lower octant; plate of four cells from cell *c*.

FIG. 80. Order of divisions in upper octants hard to determine. Dermatogen, periblem, and plerome distinct in lower octants.

FIG. 81. Periclinal followed by anticlinal in left upper octant; in the right anticlinal precedes periclinals.

FIG. 82. Cells of lower octants elongated, and beginning to form two tiers; inner cells of tier *c* greatly enlarged.

FIG. 83. Divisions in upper octants quite regular; cells of lower octants dividing transversely; periblem and plerome partly separated in tier *c*.

FIG. 84. Two tiers in lower octants nearly completed.

FIG. 85. Two completed tiers of cells in lower octants.

FIG. 86. Plerome cells of lower octants commencing to divide longitudinally; spindle indicates division of inner cells of *c* into periblem and plerome; oblique wall in *Anschlusszelle, S.*

PLATE X

Figs. 88-91, magnified 1375 diameters; *fig. 92*, magnified 890 diameters.

FIG. 88. *S. integrifolium.* In the cell below *c*, three dermatogen-terminals (*d. s.*) and a periblem-terminal (*p. s.*) have been formed by the intersection of three oblique walls.

FIG. 89. *S. integrifolium.* Dermatogen, periblem, and plerome distinct in tier *c*; periblem-terminal divided by two intersecting longitudinal walls; entire embryo outlined in *fig. 89, a*.

FIG. 90 *S. trifoliatum*. Two concentric layers of cells in plerome of lower octants and of tier *c* ; periblem and dermatogen terminals almost as in *fig. 89*.

FIG. 91. *S. integrifolium*. Anticlinal divisions in periblem-terminals ; periclinal walls in lateral dematogen-terminals (*de*), and the spindle in middle one show formation of first layer of root cap.

FIG. 92. *S. integrifolium*. Portion of a much older embryo, outlined in *fig. 92, a* ; nuclei in dermatogen cells only ; periblem and plerome separated by heavy line ; outer layers of root cap irregular.

BRIEFER ARTICLES

AN IMPORTANT WORK ON GARDEN BOTANY.

THE third edition of Vilmorin's *Blumengärtnerei* should be in every herbarium where important systematic work is done. It is one of the most notable contributions ever made to the botany of cultivated plants, but seems to be very little known in America, and therefore deserves extended notice. Even to those who work exclusively with wild plants, this work is a treasure, a much safer guide in many cases than antiquated floras, and a refuge for all sorts of puzzling names, particularly for names since *Index Kewensis*, and for cultivated plants. Nicholson's *Dictionary of Gardening*, an admirable work, is larger, and has more and better pictures, but the botanical work in Vilmorin's *Blumengärtnerei* has the advantage of a systematic arrangement. The arrangement in the former work is alphabetical as to genera and species; of the latter systematic and apparently De Candollean, but with an index of 78 pages, printed on tinted paper, and placed at the front of the work. Such an arrangement is infinitely more desirable for the student. The first volume of Vilmorin's *Blumengärtnerei* contains a review of the whole vegetable kingdom from the garden point of view, in 1264 pages, describing 245 families, 1474 genera, and 4049 species, and accounting for about 24,000 Latin names. The second volume, in its 244 pages, contains a great variety of matter, including a key to orders and genera, and 100 colored plates, four plants on a page. Other features are a glossary of botanical and horticultural terms; a review of the principles of horticulture in 38 pages; lists of plants suitable for special purposes; tabulated information concerning plants arranged in cultural groups, together with analytical keys and indexes galore. Unfortunately there are no references to original descriptions or to reliable pictures, a class of matter that is invaluable to the student or monographer, and which can be so abbreviated as to occupy little space. The botanist must not expect too much of the illustrations. They are mostly small (two inches each way or thereabouts), and designed to show habit. The trained botanist could dispense with the colored plates.

The chief value of the work to the systematic botanist is the modern and thorough spirit with which all the plants are described. It seems to have all the merits of German scholarship at its best. The editors are A. Siebert and A. Voss. Alfred Rehder, the young German specialist on hardy trees and shrubs, who is writing at the Arnold Arboretum for the forthcoming *Cyclopedia of American Horticulture*, declares that Voss has a wonderful first-hand knowledge of the plants that are actually cultivated in Germany. He knows both the live forms and the dried specimens. The "third edition" of Vilmorin's *Blumengärtnerei* was published in 1896 by Paul Parey, at Berlin. The name is an odd one, being suggested perhaps by trade reasons. Its connection with Vilmorin's *Les Fleurs des Pleine Terre* seems to be historical and commercial, as Vilmorin's *Blumengärtnerei* is very greatly superior to the early editions of the French work, although *Les Fleurs des Pleine Terre* has had a long, honorable, and useful career. The work of Voss does not exclude greenhouse plants, as might be imagined. It includes all the most important fruits, flowers, vegetables, and ornamental plants cultivated in Germany, and therefore really amounts to a monograph of the whole horticultural world from the German point of view. The nomenclature is probably too radical for the German seedsmen, who grow many of the flower-seeds that are circulated by American dealers. It would be hard to overpraise this work. In his studies for the *Cyclopedia of American Horticulture*, the writer has come to believe that Vilmorin's *Blumengärtnerei* is in many respects the best monograph of the garden plants of the world that has appeared in the nineteenth century.—WILHELM MILLER, *Ithaca, N. Y.*

THE SOCIETY FOR PLANT MORPHOLOGY AND PHYSIOLOGY.

YALE MEETING, DECEMBER 27, 28, 1899.

THIS society met, with the American Society of Naturalists and the affiliated scientific societies, at Yale University, with Professor J. M. Macfarlane as president. The following officers were elected for the ensuing year: president, D. P. Penhallow; vice presidents, Roland Thaxter and Erwin F. Smith; secretary-treasurer, W. F. Ganong. The following new members were elected: Oakes Ames, J. M. Coulter, Carrie M. Derick, B. M. Duggar, A. W. Evans, M. A. Howe, L. R.

Jones, Henry Kræmer, F. E. Lloyd, D. T. MacDougal, Conway MacMillan, G. T. Moore, Adeline F. Schively, Hermann von Schrenk, Julia W. Snow. The most important business of general interest was the appointment of a committee to endeavor to secure better reviews of current botanical literature, as referred to below.

The address of the president, upon *Current problems in plant cytology*, will probably be published in full later. The following papers were read. In each case the synopses are made by the secretary from longer abstracts furnished by the authors, the limits of space in the GAZETTE preventing the publication of the abstracts in full.

G. E. STONE: *Geotropic experiments.*

The author has attempted to settle the old question as to the angle at which gravity acts most strongly on a geotropically sensitive organism. Grass nodes and roots of *Vicia faba* were used, and experiments with dynamometers, with averages of cut plants in moist sand at different angles, and with results of after effect of stimulation were employed. All these experiments gave similar results, namely, that the horizontal position is that of greatest geotropic excitability, and that the relationship in this respect between nodes at oblique angles and those horizontal is proportional to the cosines of their angles.

D. S. JOHNSON: *The embryo sac of Saururus cernuus.*

The primary archesporial cell divides into an upper tapetal cell, and a definitive archesporial cell, which forms three potential macrospores, the lower becoming functional and developing the usual seven-nucleate embryo sac, which becomes flask-shaped. The antipodals soon become indistinguishable, and endosperm forms in the neck of the flask before any change appears in the egg. In the ripe seed only the tip of the large nucellus has been used up in formation of endosperm, while the lower part of the embryo sac is still without endosperm or nuclei.

W. G. FARLOW: *The best way of securing a good review of current botanical literature.*

The substance of this address has already appeared in the GAZETTE for January. As a result of the address, and of discussion upon it, a committee, consisting of Messrs. Farlow, MacDougal, and von Schrenk, was appointed to endeavor to secure some improvement in the reviews of current botanical literature. The committee decided to

communicate to the editors of the *Botanisches Centralblatt*, through the secretary, the opinions of the society upon this subject.

H. S. CONARD: *Fasciation in the sweet potato.* (By invitation.)

The author pointed out that fasciations are very common in sweet-potato plants, particularly those from rich soil, and that of such plants one half to one per cent. are ring-fasciated. The tubular parts, which may be two or three feet long, bear leaves and adventitious roots within, and show two bundle systems, an outer and an inner, which are alike except that the latter faces the tube cavity. They are entirely separate, but merge upward into a ring-shaped meristem, and downward the inner system gradually disappears below the end of the tube.

F. C. STEWART: *Leaf scorch of the sugar beet.*

This paper has since been published in the New York Agricultural Experiment Station Bulletin no. 162. Proofs were given that a sudden blackening and death of the foliage of sugar beets in central New York in August 1899 was due not to parasitic organisms but to scorching through excessive transpiration.

F. GRACE SMITH: *Distribution of red color in vegetative parts in the New England flora.* (By invitation.)

The author discussed the various theories hitherto advanced to explain the presence of red color in vegetative parts of plants, to test which she has observed the occurrence of red in the New England flora, classifying its distribution according to the part in which the color occurs, and the relationship of the red organ to outside conditions, and tabulating the results in percentages. In general they show that red occurs preponderantly in conducting parts, and in those exposed to light and dryness, but the results do not agree with any of the current theories; whence the conclusion is drawn that the meaning of the color must be different in different cases, or else it is determined by some factor to which we as yet have no clue.

D. P. PENHALLOW: *The morphology of certain plants from the Devonian of Europe and America.*

The author traced the history of the important fossil *Parkia decipiens*, which was first proven to be of plant origin by Dawson and Penhallow in 1891. Remains since discovered have shown that it possesses macro- and microsporangia, and that it is closely related to Marsilia and Pilularia. Another fossil of much importance is Dawson's

Nematophyton, of which no fruit has yet been obtained. The stem structure however is pseudo-exogenous, and closely like that of many Laminariæ. A remarkable and misleading crystallization effect was described. The paper was fully illustrated by photographs projected by the stereopticon.

G. T. MOORE: *Notes on the morphology and reproduction of Chlorocystis Cohnii.* (By invitation.)

This unicellular alga, growing on Enteromorpha, was described, several errors of earlier observers corrected, and some new information given. It is not always an endophyte but as often an epiphyte. The chromatophore varies from the one-sided arrangement, hitherto considered typical, to a complete lining of the wall. Two sizes of zoospores are formed, but no conjugation is probable. Discharge of the zoospores occurs through a circular opening and not through a tubular neck as formerly described.

D. T. MACDOUGAL and F. E. LLOYD: *The roots and mycorhizal adaptations of the Monotropaceæ.* (By invitation.)

The authors have investigated *Monotropa uniflora* and describe the histology of its roots, and the structure and mode of entrance of the fungus. In general the following seems true of all Monotropaceæ so far studied: the shoots lack chlorophyll and usually stomata; the usual relations of size of shoot to root are lost; the stele is much reduced and consists only of perforated vessels and companion cells; the fungus encloses the tip and penetrates the epidermis, forming special structures in the latter. The relation of fungus to host is a pure symbiosis.

R. THAXTER: *The structure and reproduction of Compsopogon.*

The author gave some account of the distribution of Compsopogon in Florida and described its general structure, calling attention to the fact that the older filaments may possess a cortex consisting of from two to four layers of cells. The details of cell structure and the normal reproduction by aplanospores were illustrated, as well as the formation of smaller aplanospores derived from sorus-like groups of superficial cells. The paper will be published in full in the BOTANICAL GAZETTE.

HERMANN VON SCHRENK: *Some diseases of New England Coniferæ.* (By invitation.)

The coniferous woods of this region are being destroyed by the mycelia of a number of fungi, chiefly of the genus Polyporus, which

act by destroying the lignin and leaving pure cellulose, or by transforming the wood into a brown brittle substance. The changes are brought about by an enzyme, and their extent is determined by the formation of decomposition products which stop the enzyme action at a certain point. Six forms of wood destruction were described, of which specimens and photographs were shown.

F. H. BLODGETT: *Vegetative reproduction and multiplication in Erythronium.* (By invitation.)

The author described the common origin, within the bulb, of the runners and annual bulbs; they come from axillary buds between the base of the stem and the inner bulb scale. He described also the development of the first bud from the seedling. From the seed the life cycle occupies not less than four years, probably longer in most cases, during which time several plants are developed.

HENRY KRAEMER: *The structure of starch grains.* (By invitation.)

The author discussed the meaning of the different appearances given in drawings of starch grains by different authors, some drawing the hilum as light and others as dark, and showed that the differences are due to the particular view (*i. e.*, focus) of the grain taken by the student. Treatment with iodine and aniline colors shows that the layers consist of substance rich in colloids but poor in crystalloids, alternating with substance rich in crystalloids and poor in colloids. The opinions of other authors as to the meaning of these layers were discussed.

RODNEY H. TRUE: *The toxic action of a series of sodium salts.* (By invitation.)

From experimental results worked out by Drs. Kahlenberg and True, the latter formulated the results presented. After studying the toxic action exerted on roots of *Lupinus albus* by a series of acids, and by their Na salts, it was determined, in view of the ionization of those compounds, to make an analysis of their toxic action into the partial toxicities due respectively to H ions, anions, and un-ionized molecules. The results were presented in detail.

F. E. LLOYD: *Further notes on the embryology of the Rubiaceæ.* (By invitation.)

A continuation of the author's studies which formerly covered only the Stellatae, but now include Diodia, Cephalanthus, and Richardsonia.

A comparative account was given of the development of ovule, embryo sac, antipodal cells, funicle, and suspensor.

J. B. POLLOCK: *The stimuli that cause the so-called "peg" or "heel" on Cucurbita seedlings.*

No abstract furnished.

W. C. COKER: *On the prothallus of Taxodium distichum.* (By invitation.)

The development of the embryo-sac, archegonia, endosperm, pollination, development of the male pro-nuclei, fertilization, and development of the pro-embryo are described in full.

A. W. EVANS: *A new type of branching in the leafy Hepaticæ.* (By invitation.)

The terminal branching in this group, according to Leitgeb, always occurs in the ventral half of one of the lateral segments cut off from the apical cell. In *Mastigobryum integrifolium* Aust. of the Hawaiian islands, however, it occurs in both lateral and ventral segments, showing that it is much less restricted than hitherto supposed.

E. B. COPELAND: *The geotropism of split stems.* (By invitation.)

Numerous experiments by the author show that if a stem be split into two equal halves lengthwise and then placed horizontally the rate of growth of the lower half is accelerated and of the upper depressed. This of course occurs in an uncut stem, but this result shows that there is no necessity for assuming a transverse transmission of the stimulus, as has hitherto been held. The paper will be published in full in the BOTANICAL GAZETTE.

HARRIET B. WINSOR and W. F. GANONG: *Some variations and correlations in the leaves of trees.*

The authors presented the results of an attempt to apply statistical methods to the study of an ecological problem, namely the influences determining the length of the petiole and the shape of the leaf. Trees were selected, and measurements made upon five hundred specimens of leaves from different positions and the results plotted in curves. The paper was offered as an illustration of method, and the studies are to be continued.

J. M. MACFARLANE: *Perennation in the stem of Lycopodium alopecuroides.*

The author showed that the branch in this species dips into the ground in autumn by geotropic growth. This part becomes colorless,

loaded with starch, and bears modified leaves, the whole forming a hook-like structure which lies dormant until the next spring, when it again comes to the surface and resumes the usual development. The peculiarity is being acquired, for some plants growing under special conditions show it but feebly.

W. F. GANONG: *The phytoecology of the Bay of Fundy salt marshes.*

The great salt marshes at the head of the Bay of Fundy offer some features differentiating them both physically and in their vegetation from other known salt marshes. The processes of reclaiming them allow many stages in the succession of plants to be seen, and this paper described the vegetation and its peculiar features from the dynamical point of view.

H. J. WEBBER: *Complications in Citrus hybridization caused by polyembryony.*

The author pointed out, and illustrated by photographs, the fact that in polyembryonic Citrus seeds, which are result of hybridization, only one of the embryos shows any trace of characters of the pollen parent while all others are like the ovule parent. Doubtless the true hybrid is derived from the fertilized egg-cell, and all the others from adventive embryos produced by nucellar tissue. The fact has a practical bearing for Citrus hybridizers in that it will be necessary to raise many embryos into seedlings before the hybrid can be found.

W. F. GANONG,
Secretary.

CERASTIUM ARVENSE OBLONGIFOLIUM.

IN 1887 Hollick and Britton, in a paper on "*Cerastium arvense L.* and its North American varieties,"[1] remarked that the variety *oblongifolium*, as it occurs from southern New York to Maryland, "is apparently confined to magnesian rocks," such as areas of serpentine and magnesian limestone, citing several localities in proof of it. They were not so confident about it in other places, though mentioning one from which the original of Torrey's *C. oblongifolium* came, "a region of magnesian limestone near Sandusky, Ohio." Having in May last found this variety — or perhaps one which agrees more closely with the variety *maximum* of Hollick and Britton — on a limestone ledge near Lockport,

[1] Bull. Torr. Bot. Club 14: 45. 1887.

Ill., I was curious to ascertain whether this peculiarity was true for this locality, being aware that many beds of the Niagara limestone on which the plants were growing are magnesian, and have been used in the manufacture of hydraulic cement, the carbonate of magnesia sometimes exceeding 40 per cent. Consulting the Geological Survey of Illinois,[2] it was found that Frank H. Bradley, the writer of the chapter on the geology of Will county, in which the ledge is situated, describes the building stones of Joliet and Lockport as "a fine grained, clinking, magnesian limestone." There can therefore be little question about the preference of the plant in this locality.

I have met with the variety *oblongifolium* but once before, having collected it in 1873 near Kankakee, Ill., where the same limestones occur. Outcrops of rock were frequent along the road by the side of which the plants grew, though the memorandum with the specimens does not say they were taken from the rocks. They were also from a locality where the beds, according to Professor Bradley, "apparently correspond with those quarried at Joliet."[3] The plants may safely be said to show their preference here also.

It was intimated above that the specimens at Lockport closely resembled the var. *maximum* Holl. & Britton, though this variety is assigned to California only. The stems are tall for the species, being 3–4·5^{dm} high, ascending to nearly erect from a short decumbent base. The leaves are lanceolate to lance-oblong, 3–5^{cm} long by 5–12^{mm} wide, acute or acutish, as long and wide as those figured in *pl. 64, fig. 2*, of Hollick and Britton's article, but not quite so lanceolate, tapering from the middle rather more than from the base. The large white flowers have petals 10–12^{mm} long; the ripened capsule is about 15^{mm} long, half or slightly more than half covered by the calyx. The plants are much more like *fig. 2* of this plate than *pl. 63*, which shows the variety *oblongifolium*. Robinson[4] remarks on the var. *maximum* "Similar robust forms of *C. arvense* have been found on the St. Clair river, Wis. (Houghton); and N. Illinois at Joliet (Boott) and Dixon (Vasey)." As the locality near Lockport is but six miles from Joliet, the forms may be identical in both places. If deemed the variety *oblongifolium*, it is not easy to distinguish the Lockport plants from those figured as the variety *maximum*.—E. J. HILL, *Chicago*.

[2] Rep. Ill. Geol. Surv. 4: 220. 1870.

[3] Rep. Ill. Geol. Surv. 4: 233. 1870.

[4] Synoptical Flora of N. America, 11: 231. 1897.

A NEW VIOLET.

Viola erectifolia.—Stems short, 2–3^{cm} long, from a single vertical tap-root: leaves elliptic to narrowly oblong or oblanceolate, entire or obscurely repand-crenate, sparsely pubescent on the veins and margins or glabrate, 3–8^{cm} long; petioles pubescent, longer than the blades: peduncles about 8^{cm} long, slightly surpassed by the leaves: sepals linear, 7^{mm} long: petals yellow, more or less tinged and streaked with purple, 12^{mm} long; the laterals with a small tuft of short stiff hairs below the middle: appendages of the anthers red and broadly ovate.

This is undoubtedly the *V. Nuttallii* of Tweedy's *Flora of Yellowstone Park*, and possibly also, in part, of Hooker's *Flora*, but it certainly is not *V. Nuttallii* Pursh, Fl. 1 : 174. The latter is a plant of the sandy plains of the Missouri and its tributaries, while the one now named is of the open woods in subalpine stations. The two can never be confused in the field, for *V. Nuttallii* has a prostrate spreading habit and several to many semifleshy roots, while the other holds its leaves and peduncles strikingly erect and all arise from a very characteristic, single, vertical root. Were it not for the differences in root characters, one might think that Hooker's figure, Fl. Bor. Am. 1 : *pl. 26*, was drawn from specimens of *V. erectifolia*. In fact it seems possible that Dr. Richardson's specimen, cited by Hooker, may be this species.

This species seems to be abundant in the mountains of Yellowstone Park and the adjacent ranges to the west. Type specimens from Henry's Lake, Idaho, June 22, 1899, no. 5481.—Aven Nelson, *University of Wyoming, Laramie.*

OPEN LETTERS.

WHAT IS PRUNUS INSITITIA?

I AM somewhat at a loss to understand the criticism which Dr. Rydberg offers in the December GAZETTE upon my conclusions regarding *Prunus insititia* Linn. as set forth in the GAZETTE of last June. He says: "If Professor Waugh had said that *P. insititia* is the same as *P. domestica damascena* . . . I would have been the last to criticise." This is precisely what I did say; and **it is a conclusion upon which I still insist.**

My reasons for this conclusion are so fully set forth in the article of last June that they need not be reiterated here. As Dr. Rydberg has appealed to the European literature, however, I may call attention to the fact that this was somewhat fully cited in my original article; and that special prominence was given to the opinions of Koch, whom Dr. Rydberg properly calls "the acknowledged authority in Germany." In citing Koch I directed attention to the peculiar fact that his opinion in 1869[1] was contradicted by his opinion in 1876.[2] In this latest study of his, which gives the clearest view of the European fruit flora with which I am acquainted, Koch says in so many words that *Prunus insititia* "is a Damson run wild." This agrees fully with the conclusion in hand.

I may add that, since writing the article which appeared in the GAZETTE of last June, I have seen the European bullace growing thriftily and fruiting abundantly in the grounds of Messrs. Ellwanger & Barry, Rochester, N. Y. It is not to be distinguished botanically or horticulturally from the damson group of plums, for which the oldest botanical name is *Prunus domestica damascena* Linn. This bullace, however, is what is generally known in Europe as *P. insititia*.

Dr. Rydberg says that *Prunus insititia* does not exist in America. That depends on what he means. The damsons are very common in our gardens, of course, and in some places have run more than half wild. Holding to the belief, then, that the damsons, *P. domestica damascena* and *P. insititia* are all one thing, I should say that, if *P. insititia* exists anywhere, it exists today in America.—F. A. WAUGH, *University of Vermont, Experiment Station.*

[1] Dendrologie 1: 95. 1869.

[2] Deutsche Obstgehölze 142. 1876.

CURRENT LITERATURE.

BOOK REVIEWS.

A cytological review.

CYTOLOGICAL literature has been accumulating so rapidly during the past few years that investigators have keenly felt the need of a critical review of the more important papers. It is extremely fortunate that Strasburger, the man best fitted to make such a review, has undertaken the work and presented the results in his masterly way, which makes the book a necessity to everyone engaged in cytological research. The volume[1] contains a brief, judicious summary of the cytological work which had appeared up to August 1899. It is more than a summary, for the author has taken this opportunity to present his own most recent researches upon these subjects, and has given the conclusions which he has reached from a fresh study of the literature and from his own work.

The reduction division.—In introducing this subject the statement is made that the existence or non-existence of a reduction division has not yet been settled, either in plants or in animals. After presenting the evidence, both for and against a reducing division, he concludes that in both the nuclear divisions concerned in the formation of spores from spore-mother cells, the splitting of the chromosomes is longitudinal, and consequently there is no reducing division. The peculiarity of the first division which follows the numerical reduction of the chromosomes lies in the fact that the chromosomes incline to an early separation and very soon undergo a second longitudinal fission. The second nuclear division which follows the numerical reduction of the chromosomes merely distributes the chromosomes, which are already marked out when the first division occurs. In the bryophytes and most of the pteridophytes the numerical reduction of the chromosomes occurs long before the process of fertilization; but in the heterosporous pteridophytes the two processes are much less widely separated, and in the flowering plants reduction of the chromosomes and the process of fertilization come very close together. This nearing of the reduction of chromosomes to the process of fertilization is plainly a derived condition caused by the reduction of the gametophyte. The author still regards the reduction of chromosomes as a phylogenetic phenomenon, which is not the cause but rather the result of

[1] STRASBURGER, EDUARD: Ueber Reduktionstheilung, Spindelbildung, Centrosomen, und Cilienbildner im Pflanzenreich. 8vo. pp. xx + 224. *pl.* 1. Jena: Gustav Fischer. 1900. *M* 10.50.

fertilization, the reduction bringing about a return to the ancestral number of chromosomes.

Spindle formation.—Nemec's recent investigations led him to believe that in vegetative cells the spindle is bipolar from the start, while in spore-mother cells it is at first multipolar. The author objects to this distinction because he thinks that the two forms intergrade. In root tips of *Ephedra major* he finds that in the early prophase of division a layer of delicate kinoplasm is formed about the nucleus, and that this layer soon collects at opposite poles of the nucleus, where it appears as a pair of caps, the filamentous nature of which is easily recognized. As the nuclear membrane disappears, threads grow into the cavity, some of them becoming fast to the chromosomes and others forming continuous threads from pole to pole. Since the threads have the same origin and same reaction to reagents, he does not approve the distinction into mantle fibers and central fibers.

Centrosomes.—The conclusion is reached that centrosomes are absent from the higher plants, although it is conceded that it would be unscientific to assert that their occurrence here is impossible. Strasburger is inclined, at present, to attribute to the kinoplasm of the higher plants all those functions which it elsewhere shares with the centrosome.

Cilia-forming organs.—The existence of blepharoplasts, which he characterizes as specialized masses of kinoplasm, should not be regarded as evidence in favor of a general occurrence of centrosomes among the higher plants. While acknowledging that it would be hard to doubt the centrosome nature of the organ which gives rise to the tail of the animal spermatozoon, he does not think it necessary to assume that the bodies at the base of cilia in animals are centrosomes. The evidence does not point to the existence of similar bodies at the base of the cilia of plant swarm spores and gametes.—CHARLES J. CHAMBERLAIN.

Classification of bacteria.

THE completion of Migula's great taxonomic treatise will be cordially welcomed by all bacteriologists. The first or "general" part which was reviewed in this journal[2] on its appearance some two years ago clearly foreshadowed the importance of the "special" part, and the huge volume of 1068 pages now before us[3] does not disappoint the expectations that were then raised. Here are brought together some 1200 descriptions of bacterial species with a more or less complete bibliography of each form, and, what is perhaps more important than all else, with an orderly arrangement by means of which related forms may be readily traced. With all its obvious defects,

[2] BOT. GAZ. **24**: 379. Nov. 1897.

[3] MIGULA, W.: System der Bakterien. Handbuch der Morphologie, Entwickelungsgeschichte und Systematik der Bakterien. Zweiter Band. Specielle Systematik der Bakterien. 8vo. pp. 1068. *pl. 18. figs. 35.* Jena: Gustav Fischer, 1900. *M* 30.

it remains true that Migula's system of classification is the best working classification now available, and the appearance of this comprehensive treatise based on his system is likely to facilitate its introduction.

In the preface, the author states that it was originally his intention to obtain cultures of all the bacteria described and to conduct extensive comparative investigations, but after nine years of labor, and with much personal sacrifice, only about half of the forms described were obtained. He somewhat naïvely continues: "Das Schlimmste war aber, dass von den ungefähr 600 Kulturen, die ich nach und nach bekommen hatte, nur ein kleiner Teil den Original-beschreibungen wirklich entsprach, die meisten Arten jedoch entweder falsch bestimmt waren, oder sich in langjähriger Kultur so in ihren kulturellen Eigenschaften verändert hatten, dass sie mit der ursprünglichen Beschreibung nicht in mindesten mehr übereinstimmten." The original plan was consequently abandoned and the description of each species is given as nearly as possible in the words of the original discoverer, even where there is reason to think that two writers have independently described one and the same microbe. It is but natural that there should be shrinking from the herculean task of welding together imperfect and incomplete descriptions, and it is perhaps more useful in the present state of investigation to possess in convenient form and in some one place all descriptions by all writers however variable they may be in accuracy and completeness. At the same time it is probable that a more ruthless hand than Professor Migula's would have eliminated some of the more obviously unfit descriptions that have been allowed to cumber his pages.

The colossal work that has been performed by Dr. Migula may be best appreciated when it is stated that descriptions of over 300 different kinds of spherical bacteria, over 700 rod-shaped bacteria and 96 spiral forms have been carefully transcribed, arranged and supplied with an excellent artificial key. If defects in manner and matter are found, they are due quite as much to the chaotic condition of systematic bacteriology as to lapses on the part of the author. Careful examination of portions of the text has failed to reveal any errors of great moment, although several faults of omission and commission have been noticed. Exception, for instance, may be taken to the statement on p. 393 regarding *B. Welchii* (*B. aerogenes capsulatus*) that the germs "seem to possess no pathogenic properties," a statement explained perhaps by the fact that no reference is given to the important study of this germ in volume I of the Journal of Experimental Medicine. We find also no notice of *B. pyogenes filiformis* (Flexner, Journ. Expt. Med. 2: 211), an organism that presents many points of interest to the systematist.

Among the more important omissions we have noticed are all the species of water bacteria described by two American writers, Wright (Memoirs National Academy of Sciences 7. 1895) and Ravenel (Memoirs National Academy of Sciences 8. 1896). However, only the continued practical use

of a text of this sort, in special investigations will show whether errors and omissions are sufficiently numerous to impair the value of a book that is certainly the fruit of monumental labor.—E. O. JORDAN.

A volume of Saccardo's Sylloge.

THE ACTIVITY of cryptogamic botanists is well shown by the recent issue of another volume supplementing Saccardo's great work enumerating all known fungi.[4] The volume has been prepared with the assistance of Dr. P. Sydow, and contains descriptions of species of fungi published during the four years closing with 1898. It was at first thought that an annual supplementary reference list of new species, omitting descriptions, would sufficiently meet the needs of working botanists, and three such lists were published in *Hedwigia*. But the great number of species constantly appearing makes the desirability of a volume like the present one beyond all dispute.

The species issued during the period of four years attained very nearly the enormous number of five thousand. This brings the total number of species described in twelve volumes of the *Sylloge*, two additional volumes being devoted to indexes, up to 47,304.

Next to the convenience of possessing all specific and generic descriptions is that of good indexes, and in these the *Sylloge* is not wanting. The present volume is supplied with a full index of species and of hosts, together with one of the genera and higher divisions contained in all the fourteen volumes.

Much critical acumen has been shown in compiling the work, and many duplications of species or of names have been rectified. There also appear descriptions of twenty-nine species not before published.

A novel and interesting feature of the work is the tabulation for easy comparison of all the genera of the *Sylloge*, arranged according to the complexity of structure of the spores. This part occupies sixty-two pages.

Altogether the work is one of great value to the student of systematic mycology. So long as new species continue to be issued by the thousand yearly, botanists cannot be too grateful for helps of this kind.

The volumes may be obtained through book dealers, or by addressing the senior author at Padua, Italy.—J. C. A.

NOTES FOR STUDENTS.

PROFESSOR ROBERT A. HARPER[5] has published the results of his researches on cell-division in sporangia. These investigations were a natural

[4] SACCARDO, P. A. and SYDOW, P.: Sylloge fungorum omnium hucusque cognitorum digessit, P. A. Saccardo; vol. XIV, supplementum universale Pars iv. Adjectus est index totius operis. 8vo. pp. 1316. Patavii, 1899. 83 francs.

[5] HARPER, ROBERT A.: Cell-division in Sporangia and Asci. Annals of Bot., 13:467. 1899.

outcome of his studies upon the ascus, and the conclusions are of great interest in relation to the problem of the origin of that organ and the group of fungi characterized by its presence. Harper studied the sporangium of Synchitrium, Pilobolus, and Sporodinia, and found the method of cell-division essentially similar in all forms.

The protoplasm of the sporangium becomes divided by "cleavage furrows" that start from the plasma membrane (*Hautschicht*) or from vacuoles. The cleavage is progressive and gradual, and in large sporangia very irregular, separating masses of multinucleate protoplasm of varying sizes. The cleavage furrows divide the protoplasm in a manner aptly termed "cleavage by constriction," and should be carefully distinguished from free cell formation. In cleavage by constriction there can be no epiplasm, and the process is initiated from the plasma membranes, either on the outside of the sporangium or around the vacuoles. This fact indicates that these two forms of plasma membranes are more closely related than may be generally believed.

True free cell formation is illustrated by the development of spores in the ascus. Here areas of protoplasm around the nuclei are cut out from the general mass of cytoplasm by the activity of the fibrillæ of an aster, and such fibrillæ are of course identical with the fibers that make up the spindle of a nuclear figure. These fibrillæ bend down and around the nucleus from the center of the aster and cut out a region of cytoplasm, which later becomes more definitely bounded by the spore wall. After spore formation there is left in the ascus a quantity of epiplasm, which, having no nuclei, must finally become disorganized.

The importance of these investigations to the problems of the relationships of ascus and sporangium cannot be stated too strongly. To one who believes firmly in the great value of comparative cytological studies as a test of relationship between groups of plants, the evidence seems overwhelming against the views advanced by Brefeld. It would be almost inconceivable that two homologous organs, such as some suppose the sporangium and ascus to be, could present protoplasmic activities of such diverse characters. The entire trend of cytological phenomena is against such a hypothesis. These investigations furnish perhaps the most striking instance of the value of cytological work as an aid and safeguard in speculation upon problems of plant phylogeny.

The paper also discusses several other topics of interest and value, but the most important conclusions are perhaps those outlined above.—B. M. Davis.

NEWS.

MR. T. S. BRANDEGEE spent last September, October, and November in collecting plants in Lower California.

DR. DOUGLAS H. CAMPBELL has been spending some time in Berlin, and is now in Egypt for the rest of the winter. His address is in care of Union Bank, London,

PROFESSOR W. L. JEPSON, of the University of California, has in preparation an illustrated book designed to serve as a popular guide to a study of the trees of California. Besides the descriptions, it will contain a key to the species, based chiefly upon the form of the leaves and other obvious or easily determined characters.

THE EDITOR of *Erythea* announces in the December number, part 1 (received January 17), that with the completion of the seventh volume *Erythea* will be discontinued. "Part 2 . . . . will contain one or two remaining articles, Erythea l'envoi, and the title page and index to the current volume. This part will be ready within two months, or as soon thereafter as possible."

AT A RECENT meeting of the board of trustees of the University of Wyoming, the herbarium connected with this institution was officially recognized as the Rocky Mountain Herbarium, and the professor of botany in the University was named as its curator. In order that this collection of plants might be more definitely designated than heretofore, it was deemed advisable to distinguish it by some descriptive name. The above was chosen because it expresses the purpose of those who are endeavoring to build it up, viz., to make it an accessible and serviceable collection of the plants of the Rocky mountains. It is established on such a basis as to insure its permanency and it is hoped that it will find among the botanists of the mountain states so many friends as to insure its rapid development. While it is intended to make the collection a general one, plants of economic importance will have particular attention, especially forage plants of all kinds, useful and ornamental trees, shrubs, and herbaceous plants. Parasitic fungi, and, as fast as facilities will permit, fleshy fungi, are to be fully represented. Such a collection will not only be of interest but of real service to the many students of Rocky mountain plants, and the cooperation of all botanists and collectors is requested. The present collection, nearly 18,000 sheets, is merely the nucleus about which the curator hopes to build, but such as it is, it is freely at the service of all botanists.

AN INTERNATIONAL congress of botanists is to be held at Paris from the first to the tenth of October 1900, in connection with the exposition. The committee of organization solicits the support of botanists of all countries and desires to have communicated, as promptly as possible, a precise statement of the general questions which they desire to have brought before the congress. It is necessary in order to make the discussions of the greatest profit in the limited time that the questions should be studied carefully before hand. Some topics which have been proposed already and have been approved by the committee are these: (1) monographic studies; (2) species, hybrids and cross-breeds; (3) unification of micrometric measures; (4) influence of the nature of the substratum on the development of fungi. The president of the committee is M. le Sénateur E. Prillieux; the vice presidents, MM. Dutailly, Mussat, and Rouy; the general secretary, M. E. Perrot, l'École Superieure de Pharmacie, Paris; the secretaries, MM. Guérin and Lutz; the members, MM. Bescherelle, Bonnier, Bornet, Bourquelot, Bureau, Camus, Chatin, Cornu, Drake del Castillo, Franchet, Guignard, Hua, Malinvaud, Patouillard, Roze, J. de Seynes, Van Tieghem, and Zeiller.

All botanists who notify the general secretary of their desire to become members of the congress and pay the fee (20 francs) are eligible. The fees are to be used to defray the cost of publishing the proceedings.

Public and general sessions, conferences and collecting trips, displays of fungi, and visits to botanical establishments are planned. Only members of the congress and delegates of French or foreign governmental departments will be admitted to other than the public sessions. Papers to be read must be sent (in full or in abstract) to the secretary before September 15. Speakers will be restricted to thirty minutes, and may not speak more than twice on the same question. The official language will be French.

FROM ADVANCE sheets of the eleventh annual report of the director of the Missouri Botanical Garden submitted to the trustees January 10, 1900, we select the following items:

The decorative features of the garden have been maintained as in previous years. In the spring a very small synoptical collection, representative of the principal natural orders of flowering plants, was installed in the central part of the garden, where it is proposed to continue it as a convenient means of enabling teachers in the public schools to demonstrate to their pupils the characters of the larger plant groups. The collection embraces 318 species, pertaining to as many genera, and representing 100 orders. . . . . The total number of species and varieties now in cultivation is 9127, a net gain of 1118. 1840 plants were presented to schools and charities. . . . . A definite count of visitors showed a total of 71,021 for 1899. . . . . The herbarium has received the most important current collections, particularly those representative of the North American flora. In addition to some 5700 specimens,

largely of Vermont plants, collected by Dr. Ferdinand Blanchard, received in the early part of the year, in December about 8300 specimens were purchased from the estate of the late Dr. A. W. Chapman, of Apalachicola, Florida, of which some 3200 specimens had constituted his personal reference collection for many years. About these Dr. Chapman wrote:

There are about fifty volumes of them, ranging in thickness from one to six inches. When I was writing the first edition of my *Flora*, these sheets were spread out before me and the plants now remaining on them are to be considered typical; but since then many have been detached, some to make up the herbarium that I sold to Vanderbilt, and some that I sent to you and to Columbia College. Scattered through the volumes are my notes, descriptions, etchings, and guesses.

Neither of these collections has yet been inserted in the herbarium of the garden. The material actually incorporated in the herbarium during the year amounts to 32,890 sheets. . . . . The present number of specimens in the herbarium is 340,350. . . . . The additions to the library for 1899 include 642 books and 172 pamphlets. . . . . The manuscript index has been increased by the incorporation of 9072 new cards. . . . . As now constituted the library contains 14,287 books and 19,175 pamphlets (total 33,462) and 253,757 index cards. . . . . It is hoped that the publication of a general catalogue of the library may be effected in the near future. . . . . There are now received at the garden library 978 serial publications, of which 91 are bought and 887, issued by 688 institutions, are presented.

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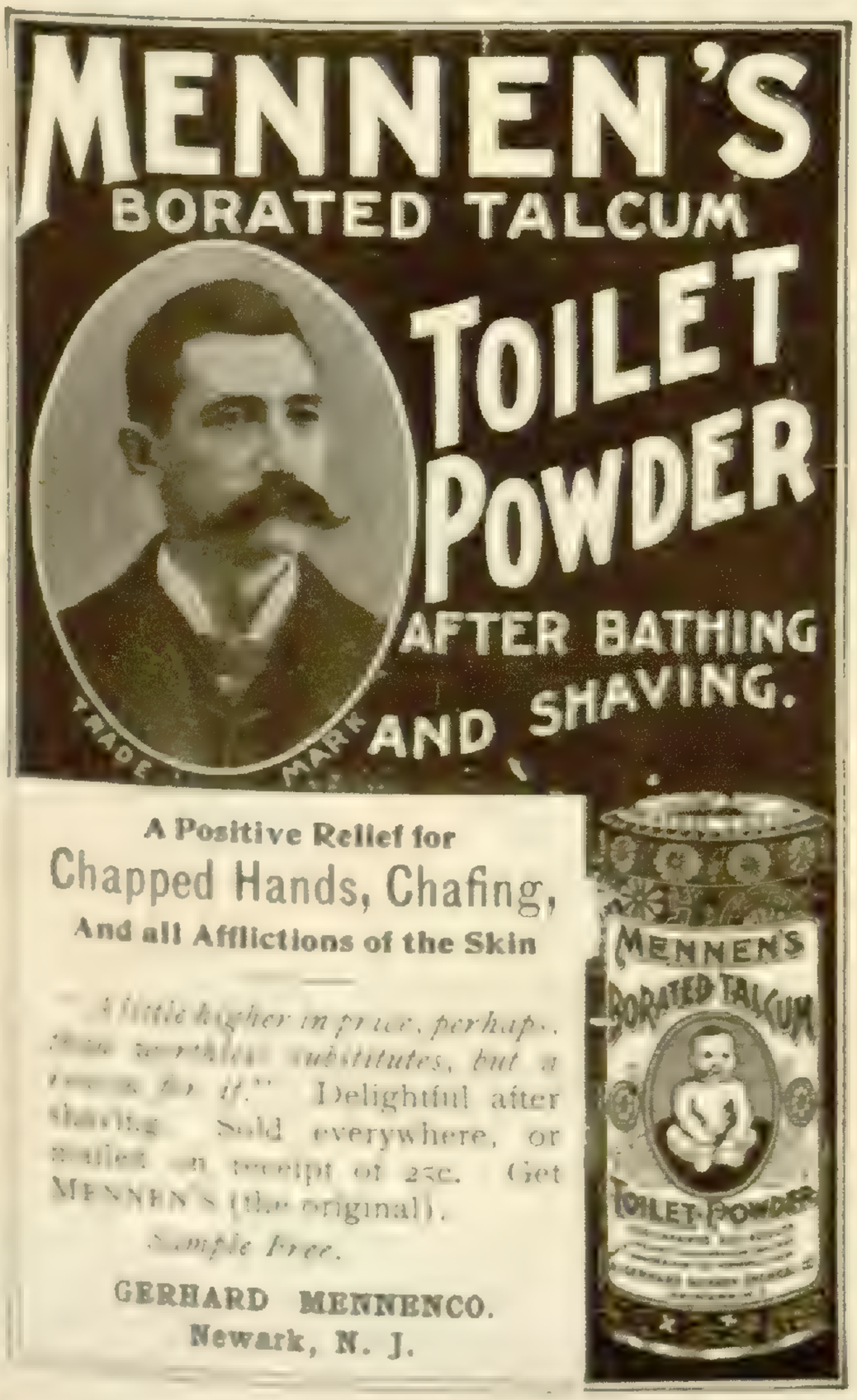
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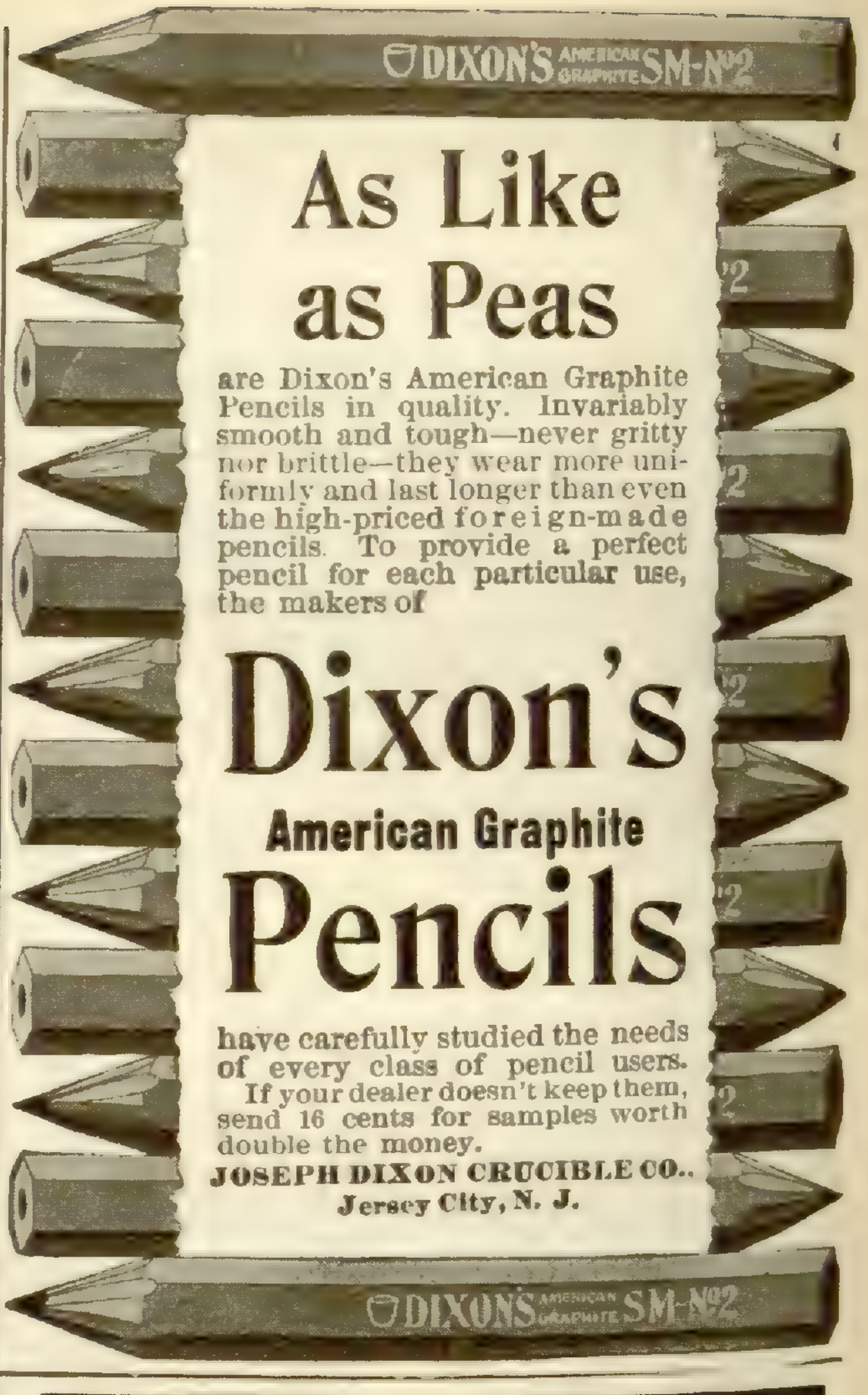

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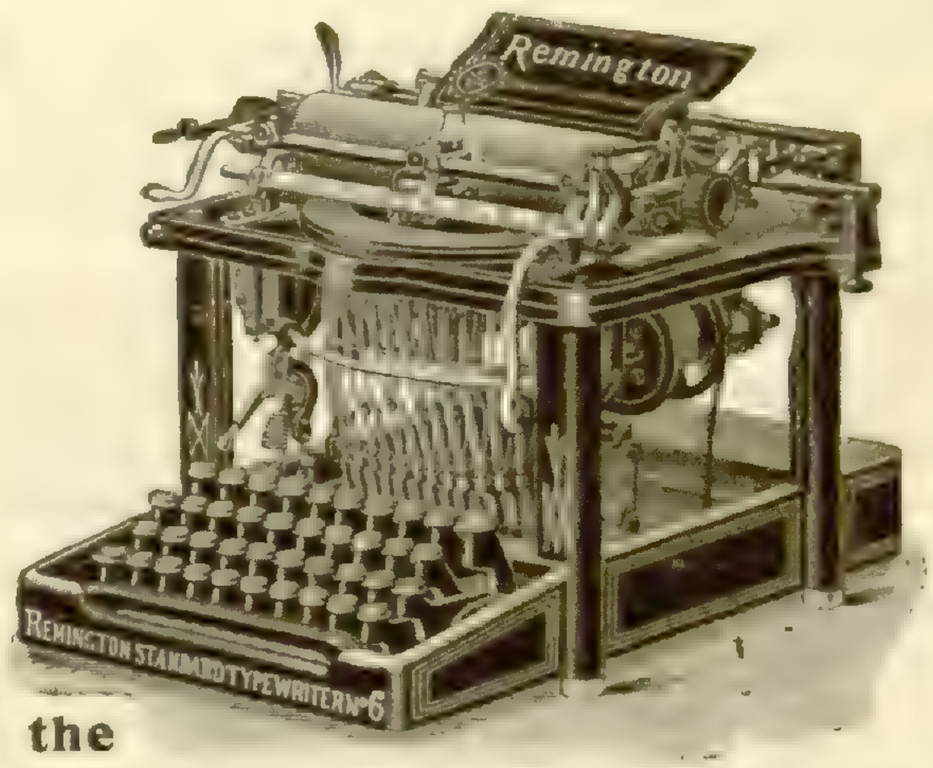

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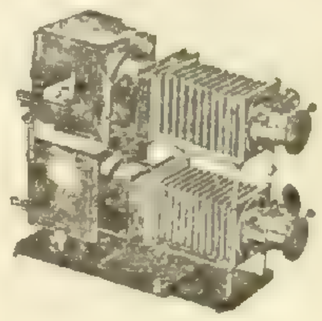

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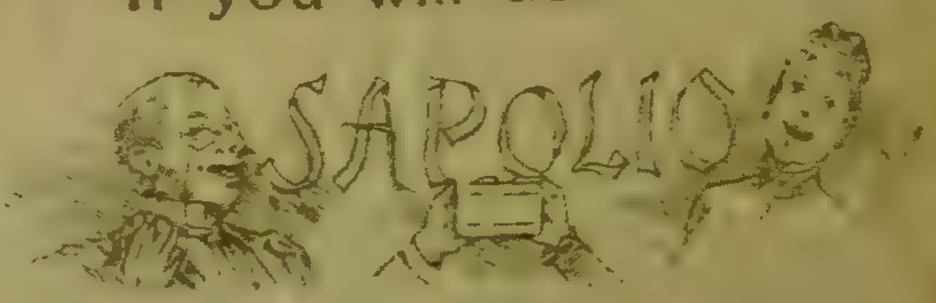

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BOTANICAL GAZETTE

MARCH, 1900

THE HAUSTORIA OF THE ERYSIPHEÆ.

GRANT SMITH.

(WITH PLATES XI AND XII)

HISTORICAL RÉSUMÉ.

THE early literature on the Erysipheæ is of historical interest chiefly. Until the middle of this century the need of exhaustive observations of the phenomena exhibited by plants had not been felt by botanists generally. The study of plant structure as a means of revealing functions had not been established as opposed to the study of structure as a means of revealing relationships in plants. Hence, though the destruction of crops by parasites had been known since the time of the Greeks and Romans, the idea of parasitism had as yet a vague and erroneous definition. By the middle of the century, however, it seems to have been quite generally accepted that parasitic fungi are nourished in some way by their mycelium, "by imbibing juices impregnated with the peculiar principle of the matrix on which they grow" (28). Thus, though this statement was extremely vague, it looked in the right direction. The mildew of the peach, rose, etc., had long been included in lists of fungi by systematists, yet the study of the structure of the fungus had proceeded only to figuring pieces of hyphæ with their conidiophores and conidia. There was little information at hand, therefore, to assist in understanding the nature of a widespread grape disease soon to be produced by one of these Erysipheæ.

Investigation received a stimulus from economic considerations, when, in 1845, a destructive grape disease appeared at Margate, England. Tucker, a gardener there, was led to a study of a mildew on the vines, because the spread of the fungus kept pace with the symptoms of disease. He published the results of his study in the *Gardeners' Journal* of 1847. The mycelium is described as ramifying through the intercellular spaces of the host-leaves and as sending reproductive branches to the exterior through the stomata. Tucker believed the fungus was a parasite on the vines. He was aided in his investigations by Berkeley (**3**) who figured and described the fungus as a new species (*Oidium Tuckeri*). Berkeley repeatedly referred (**4**) to the hemi-endophytic habit of the fungus, and as late as 1886 Worthington G. Smith (**30**) affirmed that the mycelium may sometimes be found on the interior of the leaves. If Berkeley's observations are correct, *Oidium Tuckeri* would seem to be related to Phyllactinia (p. 175) and to be distinct from the American *Uncinula spiralis*.

From England the disease spread to France and appeared at Versailles in 1848 (**9**). By 1851 it had spread all over Europe, causing much distress in vine-producing districts. Losses to owners of vineyards were so great that in France and Italy commissions were appointed to investigate the disease. Independently, Von Mohl (**33**) set for himself the task of determining whether the fungus caused or followed the disease, since Robineau (**25**) had ascribed the disease to an insect. Von Mohl did not record his methods of investigation, except to state that he examined the interior of the fruit under a microscope (**33**, p. 14). In this connection he noted the cracking of the larger grapes when covered with fungus. His search in the interior tissues of the fruit did not reveal the presence of the fungus there, so he concluded that the fungus produced its effects through the epidermal cells. Upon the epidermal cells of the young leaves, flowers, and fruit were to be seen, as soon as the fungus became visible, brown spots, which spread as the fungus spread. Young fruit upon which the fungus appeared did not

reach maturity, but withered and died. He concluded that the fungus was a true parasite on the vines and produced the disease. In 1853 Von Mohl (**34**) attempted a serious study of the weather conditions under which the fungus was able to accomplish such destruction. He examined the infested leaves more carefully and learned that the brown spots on the leaves appeared wherever the fungus was attached. At the brown spots the hyphæ produced irregular outgrowths for attachment, which he called *Haftorgane*. He strongly objected to the belief of Amici (**1**) of the Italian commission, who reported that the appearance of mildew on the vine was a proof of disease in the plant rather than the cause of the disease. This was the opinion also of Léveillé (**19**). Von Mohl cited in support of his proposition that the mildew produced the disease, the opinions of Visiani and Zanardini, of the Venetian commission. Zanardini (**38**) had observed in 1851 the protrusions by which the fungus appeared to attach itself, and called them *fulcra*. Von Mohl credits Zanardini, therefore, with the discovery of these *Haftorgane*. According to Von Mohl (**34**, p. 594) Visiani believed that he had found root-like organs arising from these *Haftorgane* and penetrating into the epidermal cells of the grape leaves. But Von Mohl did not accept Visiani's observations as correct, for he had seen only the surface organs of attachment and supposed they acted as suckers for imbibing nutriment. It seems probable, then, that Visiani was the first to see what we now call haustoria, and in his comparison of them to the roots of higher plants, he was the first to obtain a conception of those functions by which the parasite nourishes itself. Thus, as the structure of the fungus became better known, the general notion of parasitism took more definite shape.

Berkeley (**6**) believed with Von Mohl that the fungus caused the disease, and that the surface organs of attachment, which Frank (**14**, p. 556) has so well named appressoria, were suckers which drew up the juices of the host plant. Indeed, Berkeley (**5**) and subsequently other English writers applied the term fulcra to the appendages of the perithecia, and Berkeley at

least believed that they thereby absorbed nutriment from the leaves (2). Later, however, he wrote, "It is very doubtful whether they extract anything from the matrix" (7).

De Bary (12) seems to have been the first to work out the structure of the haustoria. His contributions to the subject are by far the most important and embrace the most of what is known of these organs. He applied the name haustoria, however, both to the exterior organs of attachment (Von Mohl's *Haftorgane*) and to the absorbing organs of the fungus, which he found within the epidermal cells of the host leaves. Frank (14, p. 556), at a later date, named the *Haftorgane* appressoria, reserving the term haustoria for the real organs of absorption. Of haustoria De Bary distinguished three sorts (12, p. 26): (*a*) *haustoria exappendiculata*, found in Sphærotheca, Podosphæra, and such forms of Erysiphe as have two-spored asci, the haustoria originating directly from mycelial filaments, which show little or no contortion at the points where the haustoria arise; (*b*) *haustoria appendiculata*, the haustorium arising from a somewhat hemispherical protrusion of the hypha, *i. e.*, from an appressorium; (*c*) *haustoria lobulata*, or lobed appressoria. In his Comparative Morphology (11) De Bary defined haustoria as "special organs of attachment and suction," arising in the Erysipheæ, from septate mycelial hyphæ. At this point the hypha is firmly attached to the epidermis of the host and sends the very minute haustorial branch directly through the outer wall of the host cell. Within the cell the branch enlarges into "an ellipsoidal or somewhat elongated vesicle filled with protoplasm, which in *Erysiphe graminis* is branched in a peculiar manner." The description in his Beiträge (12) is more detailed. Up to the point where the haustorial branch within the cell enlarges to form the body of the absorbing organ, the slender branch is apparently thick walled. This is not actually the case, for up to that point it is surrounded by a tube-like offset from the epidermal wall which the haustorium pierces. In cross secton, the neck of the haustorium would, therefore, be represented by a small circle, surrounded by a broad shining ring from the

host-cell wall. At the point where the vesicle begins, this collar suddenly becomes thin and becomes continuous with the outer contour of the vesicle. The diameter of a mature haustorium proved to be approximately equal to the diameter of the mycelial thread. When the vesicle is young, De Bary says it has a very delicate wall, but an old haustorium has a colorless double-contoured wall within which is minutely granular protoplasm, either homogeneous throughout, or consisting of a dense ball in the middle surrounded by transparent granular protoplasm. In cases where the haustorium is extremely old the contents consist of shining, oily masses. Not infrequently, if the epidermis to be penetrated is thick or if the penetrating tube ceases to grow, he observed that the haustorium does not enlarge into a vesicle, but is surrounded by a cone-shaped or knob-shaped protrusion of epidermal wall projecting into the cell. De Bary also examined grapes and grape leaves infested with *Oidium Tuckeri*. He seldom found the haustoria normal in the fruit of the grape, but usually he found only the penetrating tubes surrounded by the cone-shaped ingrowths of the browned host-cell wall extending into the epidermal cells, as just described. Even in cells containing mature haustoria he found no great disturbance wrought in the cell wall, the cell protoplasm, or fluid contents. He frequently observed, however, in otherwise normal cells, that the haustoria are surrounded by thick, irregular masses of protoplasm belonging to the host-cells, which ammonia or KOH would remove sufficiently so as to allow the true haustoria to be seen. Gradually, the browning observed on the exterior of the epidermis spread to the contents of the infested cells, but he did not observe such extreme browning as was described by Von Mohl. It is to be noticed that all of De Bary's studies of the haustoria were made from the surface of the leaves.

Büsgen (10) refers to haustoria in reporting his observations on the effects of chemotropic and other stimuli upon the germinating tubes of fungi. He germinated conidia of *Erysiphe communis* from leaves of *Polygonum aviculare* on slides under cover glasses. In some cases he used sections of infested leaves

in weak nutrient solutions. He was able to obtain appressoria-like organs where the filaments came in contact with the cover glass, but the germinating tubes had a very limited growth and soon perished. His results with the leaves indicated chemotropic reactions in the filaments. As a whole his experiments on the Erysipheæ were not directly successful and they bear little relation to the haustoria themselves. Reference will be made to this paper again in discussing Phyllactinia.

Galloway (15) devotes a short paragraph to haustoria in an account of his observations on the development of *Uncinula spiralis* and figures them in much the same way as De Bary. Harper very briefly describes the haustoria of *Sphaerotheca Castagnei*, and he gives but a single figure (17). Palla (24) has recently investigated Phyllactinia on Berberis and Corylus, but he concerns himself rather with the habit and structure of the mycelium than of the haustoria. For the minute points of structure his methods are inadequate, as he himself intimates (p. 70).

It will be seen from this brief résumé of the literature that the minute structure and especially the development of the haustoria are almost entirely unknown.

METHODS.

Four fixing solutions were experimented with and their respective merits were compared: Flemming's fluid (stronger solution), Merkel's solution, chrom-acetic acid (0.7 per cent. of the former and 0.3 per cent. of the latter), and a saturated solution of mercuric chlorid in 1 per cent. acetic acid. Flemming's fluid proved the most reliable and satisfactory. In those cases in which it blackened the tissues, the sections, after having been attached to the slides, were bleached for twenty-four hours in hydrogen peroxid before staining. Merkel's solution was frequently satisfactory, but it proved hardly as reliable as Flemming's. The other two solutions were far less useful. The sections of leaves were cut 6–7 μ in thickness and were fixed to the slides by the well-known albumen and distilled water methods. They were cleared in clove oil and mounted in Canada balsam.

Some difficulty was experienced in sectioning those leaves which contain large crystals of calcium oxalate, as Corylus and Xanthoxylum, because these crystals frequently caused the destruction of the ribbons. For that reason, the side of the leaf bearing the fungus was usually turned toward the knife in cutting, unless the fungus was amphigenous.

All staining was done on the slide. Wisselingh (**37**) finds in fresh material that chitin is present in many places as one constituent of fungus cellulose. In the Erysipheæ, chitin appears in the perithecia, appendages, mycelium, conidia, and conidiophores. He does not mention haustoria in this connection and finds no characteristic stain for walls containing both cellulose and chitin ; congo-red, however, in neutral and ammoniacal solutions, stains pure cellulose intensely, while if chitin is present also, the color is not dark, unless the chitin be transformed to mycosin.[1] Mangin (**21**) found pectin quite generally present in fungus cellulose and employed ruthenium-red as a characteristic stain. Wisselingh (**37**, p. 632) was able to remove the pectin from cell walls containing it. Mangin did not investigate this question and Wisselingh denies the presence of pectin in the Erysipheæ. My own results confirm this view. With ruthenium-red the fungus would not stain at all, though the middle lamellæ of the cells of the host-leaf gave the pectin reaction. The most characteristic staining obtained in the fungus, in the use of congo-red (neutral and alkaline solutions) and methylene-blue (neutral and acid solutions), was an intense staining of the ascus wall in the perithecium. Wisselingh does not mention this as a part containing chitin, and, since the remainder of the fungus seemed to give the chitin reaction by refusing to stain deeply with congo-red, it is possible that the ascus wall is composed of pure cellulose.

The walls of the haustoria do not show any reactions to stains that would indicate that they contain any different material from the remainder of the fungus. Flemming's well-known triple stain, safranin, gentian-violet, and orange-G, proved

[1] He used a modification of Gilson's method (**16**).

very satisfactory. By this stain the nucleoli of the fungus and host are stained red, the chromatin blue, and the ordinary protoplasm orange. Fungus nuclei in the process of division take the violet stain readily, but in a resting condition they possess chromatin in very minute masses. The most of the nuclei shown in the accompanying figures had to be under-stained with violet in order to prevent the over-staining of the host-tissues. The nuclei are represented as containing conspicuous chromatin granules, because in properly stained nuclei the granules are differentiated.

ERYSIPHE COMMUNIS.

Erysiphe communis proved very favorable for study, and since Erysiphe, Sphærotheca, Microsphæra, and Podosphæra appear to agree closely in respect to their haustoria, the fungus on *Geranium maculatum* will be described as a basis for comparison. *Fig. 8* represents such a case as De Bary described. The hypha from which the haustorium originated is not shown, as the mycelium is very easily so far separated from the leaves in the process of fixing and imbedding as to destroy the connection between haustoria and hyphæ, a fact upon which De Bary (**12**, p. 27) and Harper (**17**) comment. The absorbing organ is seen to consist of a slender, proximal portion, the neck, penetrating the epidermal wall of the cell, within which it enlarges into a vesicular, distal portion with a thin wall. On the interior, the vesicle is filled with a delicate, spongy protoplasm differing in no visible particulars from the protoplasm in the mycelium. A mature haustorium always contains one normal nucleus, a fact to which De Bary does not refer. He probably saw it as the "thick ball" surrounded by transparent protoplasm, to which reference has been made. Harper (**17**) for the first time mentions the nucleus in his paper. *Fig. 11* represents the only case I have seen of a haustorium with two nuclei. This haustorium is also septate and such septa occasionally present themselves (*fig. 13*). *Figs. 8, 19*, etc. show in longitudinal section that the ingrowth from the inner surface of the wall of the host-cell

surrounds and accompanies the neck for a distance, as De Bary reported. It seldom extends down to the body of the haustorium, however, and sometimes is absent altogether (*fig. 16*). The collar from the cell-wall is somewhat different from the wall from which it takes its origin, and usually stains little, while the remaining portion stains with safranin intensely. The outer surface of the neck adheres closely to this collar, the outer boundary of which is represented by the middle circle in *fig. 17*.

But *fig. 8* does not represent the usual conditions in one particular. Almost always a mature haustorium is surrounded by a thick, sheath-like layer which, De Bary says, belongs to the protoplasm of the host-cell. It is clear that, by the use of hand-cut sections of fresh or alcoholic material and by a study of the haustoria from the leaf surface, he was not able to make out the structure of this sheath fully. De Bary describes it as an irregular mass; but it is not extremely irregular and is bounded by a very thin membrane of about the delicacy of the plasmic membrane of the host-cell. In *fig. 9*, for example, the middle cell contains an optical section of a haustorium. Within the center lies the relatively large nucleus with its red-staining nucleolus and fine chromatin granules. Surrounding the nucleus is the spongy protoplasm staining orange. The haustorium-wall surrounds this protoplasm. Exterior to the haustorium are the contents of the sheath described by De Bary as belonging to the protoplasm of the cell, while bounding the whole, in contact with the contents of the host-cell, is the delicate limiting membrane of the sheath itself.

The substance of this sheath looks like protoplasm at first glance and stains with orange, but it is not vacuolated like protoplasm. It consists of a dense, homogeneous, finely-granular mass, most frequently gathered into lumps of varying outline, which appear very slightly granular (*figs. 9, 11, 16*). Rosen (**26,** p. 258) observed in *Puccinia asarina*, growing in the intercellular spaces of Asarum, that the branched haustorium was connected with the nucleus of the host-cell in the majority of cases, and either adhered closely to it or entered it with disorganizing

effect. Harper (**17**, p. 664), disagreeing with De Bary, thinks that among the Erysipheæ this peculiar sheath is, as in Puccinia, the disorganizing nucleus of host-cell. The delicate bounding membrane would, therefore, be the nuclear membrane.

I have not found evidence of such a relation between haustorium and host nucleus in the Erysipheæ. In the examination of many sections in searching for stages in the development of the haustoria, it becomes more and more clear that the host-nuclei and haustoria are indifferent to each other. The sheaths are present around the haustoria even if there are several infesting one cell, as frequently happens. In such cases, if the cell is not so full of haustoria as to obscure the cell contents or crowd the nucleus, that body can be seen in a more or less normal condition. In the cells of hairs which are large enough to contain several haustoria easily, the sheath of each can be seen, while the host-nuclei occupy distant positions in the cells. The sheaths are to be accounted for in another way, as will be shown subsequently.

In most of the figures the host-nuclei lie at a greater or less distance from the haustoria. When, as in *fig. 16*, the connection between the two is close, the nuclei are more or less disorganized. But the cases figured make the proportion seem much too large to be in accordance with the facts. The sheath is not usually bounded by a tensely stretched membrane (*fig. 7* represents a special case), but by a membrane having a more or less irregular outline in section, beginning where the cellulose collar stops. The orange-staining contents are usually present in more or less abundance, except in *Erysiphe graminis* on Poa, where only the sheath is present and is sometimes inconspicuous.

The outer walls of the epidermal cells have an affinity for the safranin stain, but the collar about the haustorium neck stains much more delicately with it. In *fig. 10*, shown because the cell was plasmolyzed, the collar is distinct from other parts and appears under the microscope very slightly stained with safranin. Again (as in *figs. 16*, *21*, and frequently in other figures), the reaction is such that the neck of the penetrating organ is

distinctly visible and its slenderness appreciable; whereas, if it were not for this circumstance, the size of the tube would frequently be exaggerated.

Nordhausen, in experimenting with Botrytis, Penicillium, and Mucor (**23**, p. 38), observed a marked browning of the epidermal cells in contact with the germinating spores, which always preceded penetration. He thinks (p. 7) that the phenomena of browning and subsequent death of the cells are due to the production of some poison during the germination of the spores. Von Mohl (**34**, p. 592), De Bary, Frank (**14**, p. 556), and others mention this browning in the Erysipheæ. In the stained sections this brown color is not distinguishable, though the cell wall around the point of penetration is more or less altered and dissolved. Seen from the outer surface of Poa (*Erysiphe communis*) and Eupatorium (*Erysiphe Cichoracearum*), there is an area surrounding the point of penetration which is entirely colorless, clear, and shining. The remaining portions of the epidermal wall stain with safranin. The outer surface of the colorless area is usually depressed also, the depression being deepest at the point of penetration, as though a part of the cellulose had been dissolved away. This dissolution of the cellulose suggests that the Erysipheæ probably produce an enzyme suited to this work.

In the sections of Geranium leaves the safranin stain frequently makes evident the beginning of penetration. The first intimation of the process is a deep staining of the inner surface of the outer wall of the cell immediately under the point where the hypha comes in contact with the epidermis (*fig. 1*). This staining, however, is to be seen occasionally at the cross-walls of the epidermis, where haustoria have never been produced. It is possible that it is this deeply staining spot which shows the brown color in fresh material.

The next step to be observed in the development of the haustoria (*fig. 2*) is the thickening of the epidermal wall toward the interior over an area coinciding roughly with the clear space already mentioned (*fig. 17*). Nordhausen (**23**, p. 17) observed

a slight swelling of this kind with Botrytis on Tradescantia, Mnium, etc., but Ward (**35**) observed with the same fungus (apparently), which produced the lily disease he described, such an extraordinary swelling of the walls of the host that a large part of the lumen of the cells was filled. Nordhausen believes that Botrytis lives on the protoplasm of the poisoned cells chiefly. Ward is of the opinion that the fungus causing the lily-disease lives also on the gelatinized walls. Erysiphe appears to produce not so much a swelling of the wall of the cell as the addition of new material to its inner surface, for the collar of the haustorium, formed from a part of this thickening, is dense and remains as a permanent structure in the cell.

At the same time that the wall of the cell is thickening, growth of the penetrating tube is proceeding. Its distal end enters the wall, and, just at the point where the reddening of the wall originally appeared (*fig. 2*) a very slight enlargement of the tube occurs, accompanied still by the reddening on each side (in longitudinal section). But this effort does not bring the point of the tube into the lumen of the cell, for the thickening of the wall keeps pace for a time with the growth of the tube. This tube is extremely minute. For Botrytis Nordhausen (**23,** p. 39) found it to be one fourth of the diameter of the ordinary hyphae. Miyoshi (**22**)[2] has shown that the membrane to be penetrated affects the size of the tubes. Thus, when collodion was used for a membrane, the tubes actually increased in diameter, while with an onion skin there was no change in the size of the tube. Ward's observations on this point agree with Nordhausen's. In all of the Erysipheæ the tube is much smaller, as the figures show, and it is interesting to note that the nucleus of the absorbing organ must in some manner make its way through this minute passage.

The tube (*fig. 3*) continues its growth through the increasing or (as Ward thinks for Botrytis) swelling cellulose, a part of which remains permanently encircling the neck of the mature

[2] Die Durchborung von Membranen durch Pilzfäden. Jahrb. f. wiss. Bot. 30: 280. 1895.

haustorium as the collar so frequently mentioned. De Bary (12 p. 26) probably saw something of this phenomenon in the form of the knob-shaped papillæ in the cells as mentioned above. He saw the structures in cells with thick epidermis and in what he thought were no longer growing haustoria. Because of the closely connected series of stages which it is possible to secure, it is evident that these are not old, disintegrating haustoria. Rather they represent the early stages of penetration. At any rate, if they represent dead haustoria, they reveal the outlines of the cellulose parts none the less, and so tell the story of development. Just what significance there is in this thickening of the host wall cannot be conclusively determined without experiment. The wall increases not only in bulk, as Ward found, but in quantity, as has been mentioned. That there soon *does* appear to be a disintegration of a portion of this ingrowth, will be seen presently. There are not data at hand to determine whether the penetrating tube, by means of some chemical substance, excites the cell protoplasm to unusual activity in the production of cellulose over the region of penetration, or whether microscopically small needles would cause such a production mechanically. Again, it is possible that the stimulating agent is the atmosphere acting through the wall at the point made thin by the work of the fungus. There would then be the same reason for this local thickening as there was for the original production of a thick outer wall in the first place.

Soon the tube, growing with increasing rapidity, overtakes the cell in what may be its efforts to protect itself from injury by the fungus. Whatever may have been the stimulus which produced it, the thickening of the wall ceases after a considerable ingrowth, U-shaped in outline, has been formed. The first appearance of disintegration is now to be seen in it. The distal end no longer has the appearance of cellulose such as is found in the cell wall and in the clear basal portion. Some change has been wrought in it which has altered its appearance and its reaction to stains. This end (*fig. 4*) may now be stained slightly orange, and it is slightly and minutely granular. No

sharp boundary separates the proximal from the distal end. The granular character of the latter gradually lessens toward the dense proximal end, which stains very slightly with safranin. The still slender penetrating tube is to be seen piercing this basal portion and extending into the now disintegrating distal extremity. It is to be observed that the plasmic membrane of the cell, by means of which the ingrowth has been formed, passes up the side and over the end of that structure. The gradual disintegration of this ingrowth of cellulose thus forms the early stages from which the true structure of the haustorium sheath can be understood.

The growth of the haustorium now continues with accelerated speed. It will be seen in *fig. 5* that the penetrating tube has taken a straight course through the cell wall and the basal portion of the papilla, for a distance approximately equal to the length of the collar in a mature haustorium. From that point on to the point where its growth was checked by the fixing fluid, the tube has pursued a rather tortuous way or else the distal surface of ingrowth has offered some resistance to the progress of the tube. The end of the tube has begun to enlarge into the vesicle which forms the body of the mature haustorium. The nucleus has not yet started in. The whole distal portion of the cellulose surrounding the end of the tube is now distinctly granular and takes a deep orange stain. The staining of the wall on the line of its original inner surface is no longer visible. The hypha from which this tube originated is sufficiently enlarged and flattened to fall within De Bary's class of *haustoria appendiculata*, peculiar to forms of this genus possessing two-spored asci. *Erysiphe communis*, however, would be a species without appressoria, according to this classification.[3]

[3] It seems questionable whether much dependence can be placed upon forms of appressoria in systematic determinations, such as the separation of *E. Galeopsidis* from *E. Cichoracearum* (Ellis and Everhart, N. A. Pyrenomycetes 14. 1892). The former is supposed to have lobed appressoria. The varieties of *E. Galeopsidis* used in this investigation do not appear to show more conspicuous appressoria than *fig. 5* represents. Between the appressorium and the epidermal wall is drawn in outline a cushion-like structure which stained red. This was the only case of the kind observed, and its significance is unknown. In *fig. 5* again the nucleus of the host is on the basal wall of the cell.

In *fig. 6* the absorbing organ is in a thick-walled epidermal cell in the region of the midrib of the leaf. The vesicle has continued to enlarge until it has reached the form, but not the size of a mature haustorium. It would never have possessed the usual sheath, because by pressure or fermentative action, or by both, it has escaped from its enclosing cellulose, which has approximately the same structure as the disintegrating papilla shown in *fig. 5*. The collar at its base, therefore, consists of the entire ingrowth and not of its basal portion only, as is common in most mature haustoria. It does not as yet contain a nucleus. Outside of the cell is shown a piece of mycelium containing numerous safranin-staining bodies which are probably food material of some sort.

In *fig. 7* is shown a nucleus making what appears to be an unsuccessful attempt to enter the haustorium. The hypha has been broken away so far that none of the pieces lying above the cell could be identified surely as belonging to the haustorium. The nucleus seems to find some difficulty in entering, either because of its size or, possibly, because the darkly staining material lying in front of it offers some resistance to its progress. The passage of the nuclei into the haustoria is naturally most difficult to see. This unsatisfactory example is the only case observed. The haustorium must attain nearly its full size, therefore, before it is provided with a nucleus. Up to this time it contains only highly vacuolated protoplasm. It is difficult to find cases which show nuclei in position to pass down the penetrating tubes into the haustoria. The few cases observed have been figured, but it cannot be said conclusively that these are the nuclei which were ultimately to find their way into the haustoria. The nuclei of the hyphæ are sometimes greatly elongated and narrowed (*fig. 14*). It must be in such a form that they make their way into the tube.[4] *Fig. 7* is instructive in another respect. The sheath of the haustorium contained, when the material was fixed, nothing but fluid. The contents have been entirely consumed. But the bounding membrane is

[4]See also figures by Harper, 17, p. 663.

stretched and turgid, and none of the solid contents of the host-cell approaches nearer to the haustorium than the outside of this *sheath-membrane*. That this membrane is so tensely stretched shows that it was filled with a liquid when the material was fixed. It, therefore, possessed osmotic qualities similar to the plasmic membrane of the host-cell. It has been mentioned that the plasmic membrane of the cell, by the activity of which the cellulose papilla was produced, extends over the papilla (*fig. 4*). In *fig. 7* this plasmic membrane is stretched and enlarged extraordinarily until its origin would not be easily recognized.

From what has been said on the development of the haustoria, it is easy to understand the nature of the sheath around the haustorium, with its bounding membrane. That is, it does not belong to the protoplasm of the cell as De Bary supposed, nor is it the host-nucleus as Rosen observed in *Puccinia;* but the contents of the sheath consist of disintegrated cellulose from the distal end of the cellulose ingrowth through which the haustorium has made its way. The bounding membrane of the sheath, on the other hand, is the plasmic membrane of the host-cell stretched and greatly enlarged by the osmotic forces involved. In so far only does the sheath belong to the protoplasm of the cell, and not at all in the sense which De Bary had in mind. There is abundant evidence from various sources to support the view just stated. Marshall Ward (**35**, p. 356) has shown that Botrytis produces a swelling and gelatinization of the cell-walls of the lily leaves. Ward found that the fungus was able to live on this disintegrated cellulose. It is well known that certain fungi produce ferments which are able to digest cellulose. Ward found such a ferment in Botrytis (pp. 343–346). So also Beyerinck (**8**) found that *Coryneum Beyerinckii* makes use of a dissolving ferment. Nordhausen (*l. c.*, p. 38) has shown that Botrytis, Penicillium, and Mucor can enter a cell-wall and grow through it parallel to its surface for comparatively long distances. Indeed, this power of disintegrating cellulose is probably generally possessed by fungi, parasitic and saprophytic. The Erysipheæ probably have such a ferment. The partial

dissolution of the epidermal wall of the host about the point of penetration has been mentioned. The penetrating tube makes its way through a long ingrowth of cellulose before it expands into a mature haustorium. The mature organ shows no unmodified host-cellulose surrounding it except the collar around the neck of the haustorium. The distal portion of the ingrowth partially disappears in the development of the penetrating tube. During the disappearance, it undergoes changes which materially alter its microscopic appearance as concerns structure and its capacity of reacting to stains. It becomes decidedly granular and takes an orange stain, whereas, in the beginning, the entire ingrowth was of the same consistency as the collar, and took the safranin stain slightly. By the time the penetrating tubes begin to enlarge, these changes are conspicuous. The tube may finally break through the cellulose and develop without any sheath. But usually some of the cellulose remains as the granular masses of the sheath. It will be shown subsequently that, under certain conditions, the haustoria of *Uncinula Salicis* have no sheaths, and the sheaths of *Erysiphe graminis* on Poa do not show any contents in the older stages nor are the sheaths always present.

The extremely minute size of the penetrating tube has been mentioned. The amount of fermentative action, of which the young haustorium is capable at first, is, therefore, only sufficient to provide for the onward growth of the tube. The cell succeeds in laying down cellulose ahead of it for a time. The circle of the fermentative effect has not at first a long radius. The distal end of the ingrowth is the first to show signs of dissolution. It becomes granular there. As the absorbing organ attains larger growth the digestive powers of the fungus become more effective, and that part of the collar coming within the sphere of influence of the ferment is gradually attacked and partly dissolved.

It is interesting to find that the membrane by which the sheath is bounded in a majority of cases is contributed from the plasmic membrane of the host-cell. The plasmic membrane is

not ruptured by the ingrowth of cellulose. Rather the ingrowth is caused by the activity of the membrane, the area of which enlarges with the thickening of the wall. The plasmic membrane is still recognizable when the haustorium begins to enlarge at its distal end. It still maintains its osmotic properties at the stage represented by *fig. 7*. In most cases it remains bounding the masses of disintegrated cellulose which constitute the contents of the sheath. *Fig. 7* represents the membrane stretched and firm from the osmotic forces at work in the nutrition of the fungus. At a later stage it usually suffers injury and sometimes dissolution.

This fungus is not capable of producing the extraordinary dissolution of cellulose which Ward found in the case of Botrytis. Its supply of enzymic material seems to be limited. The sheaths are, therefore, usually present, though on rare occasions they are not, as in *figs. 8* and *12*. Certain haustoria of *Uncinula Salicis* do not possess sheaths and, as will be seen, this species has a greater digestive capacity. Nordhausen (**23,** p. 23) found in infecting leaves with spores of Botrytis that heavy dews so weakened the enzyme of the fungus that penetration was impossible. It seems probable that, when the cell-sap of Geranium begins to be absorbed by the young haustoria of Erysiphe, the enzymic material is weakened or largely reabsorbed. Thus it can be seen how the sheaths with their bounding membranes are possible and how, as De Bary observed long ago, the host-cells may escape with so little injury. From the time when the haustoria begin to absorb actively, the further digestion of the cellulose papillæ largely ceases, and though their bounding membranes collapse, they are usually not completely digested, being protected by the cell-sap. In *fig. 8* the sheath is all digested down to the collar. In *fig. 19* the haustoria succeeded in penetrating the wall of the hair, of which the cell forms a part, before the plasmic membrane could build up papillæ to impede the progress of the tubes. The digestive capacity of the haustoria is not entirely constant, so that we find sheaths in various stages of disorganization.

ERYSIPHE GRAMINIS AND OTHER SPECIES.

The absorbing organs of *Erysiphe graminis* on *Poa pratensis* deserve description. It has long been known that the haustoria of this species are "branched in a peculiar manner." This fungus grows very luxuriantly on the grasses and fills the epidermal cells full of large branched haustoria. A shining, colorless area occurs around the penetrating tube (*fig. 17*) which is slightly larger than in *E. communis*. The colorless area is slightly depressed, as already mentioned. The collars of cellulose are relatively thick also. *Fig. 19* represents nearly the maximum thickness for the collars in Poa. The body portion of the absorbing organ is always approximately cylindrical or ellipsoidal, with finger-like projections growing out from the ends or sometimes from only one end (*figs. 19, 21*). A large nucleus lies near the middle, and in either end, in mature examples, there is a large vacuole. The branches are also vacuolated. The body is not always symmetrical with respect to the neck (*fig. 20*) but the neck may be near one end from which, even then, branches may arise. The development of the haustoria of this species was not followed, but in none of the mature examples have the sheaths possessed any granular contents as found in *E. communis* and elsewhere. The sheath-membranes are usually present, though they exhibit great irregularities. Sometimes they are not to be seen except for a short distance; sometimes they completely surround the haustoria, being discernible even down between the branches, At other times the branches penetrate the sheath. The protoplasmic contents of the epidermal cells are usually scanty. It seems impossible that the cell nucleus should escape destruction when the haustoria are thus provided with long branches. But the same indifference to the nucleus exists here as in *E. communis*. Even when a cell contains several haustoria, the nucleus is usually unmolested, and is often as normal in appearance as in uninfested cells. This form of absorbing organ may be looked upon as the result of a special effort of this species to obtain abundant food. The heavy growth of mycelium and the immense number of conidia produced by this species

show the success it has attained. Many of the appressoria of this species agree with De Bary's *haustoria appendiculata*. *Fig. 19*, being a side view, shows only one outline of the organ of attachment. Long infested blades of Poa show signs of injury from the fungus. "In California it has been destructive to wheat" (13).[5] Certainly these haustoria give the impression of activity not gained from other Erysipheæ.

The habit or structure of the other species of Erysiphe studied do not differ so much from the account given of *E. communis* that a detailed description is necessary. Basal (and even higher) cells of hairs are especially favorable places for the study of haustoria. *Fig. 16* represents such a cell from a hair of *Eupatorium perfoliatum* infested by *Erysiphe Cichoracearum*. The nucleus of the cell lies between two of the haustoria and seems to be disorganized. The cell is slightly plasmolyzed. The dark globules (stained red in the sections) do not seem to be degeneration products due to the action of the fungus, for the cells in uninfested leaves contain them. They are probably due to the fixing reagents. This plant, it is well known, contains a volatile oil and a resin. It is probable that the globules are related to these substances. It is very common to find such products as these in the autumn, when this material was gathered.

UNCINULA SALICIS.

Uncinula Salicis on *Salix discolor* exhibits peculiarities in its appressoria and haustoria, which apparently have not been reported heretofore. De Bary (**12,** p. 27) mentioned the lobed appressoria (*haustoria lobulata*) of this species, then called *U. adunca*, but he did not report any peculiarities in the haustoria; and Galloway examined *U. spiralis* (*U. necator*). It has frequently been stated by De Bary and others (**12**; **32**; **36**; **20**; **18**; **14,** p. 555; **13,** p. 2; **19**) that the Erysipheæ always confine their absorbing organs to the epidermal cells of the host. Berkeley, it has been mentioned, believed in the hemi-endophytic habit of

[5] The writer has never found it difficult to collect material, with ascospores developed, in August and September.

some of the powdery-mildews, and Palla (**24,** p. 68) has recently shown that Phyllactinia has intercellular hyphæ. *Uncinula Salicis* also offers a striking contradiction to that old conception, but the method by which this fungus reaches the interior tissues of the leaves is different from the one Phyllactinia employs.

Uncinula is amphigenous on the leaves of the willow. Its appressoria are lobed, as De Bary affirmed. The mycelium is entirely external. On the upper surface of the leaves the lobed appressoria give rise to penetrating tubes which enter the epidermal cells. All of these tubes do not develop in the epidermal cells into haustoria. An examination of a cross-section of the willow-leaf shows that the epidermal cells are very abundantly infested with haustoria, but in addition, numerous slender bars can be observed reaching from the outer walls across the epidermal cells to their inner walls. The bars give the cells the appearance of possessing trabeculæ. The haustoria in the cells frequently hide the outer end of these structures, but in following their course to the inner wall, haustoria may sometimes be observed in the palisade cells of the leaf. The bars are the penetrating tubes, or the necks, of these subepidermal haustoria. When the penetrating tubes reach the palisade cells they enlarge into haustoria not unlike the ones described for *E. communis*, possessing the sheaths and nuclei. Several tubes may pierce the outer epidermal wall close together and take different directions across the cells. Of the tubes which penetrate the outer wall of the epidermal cell close together, some may enlarge immediately into haustoria, while others may pass to the palisade cells. This crowding and confusion makes it difficult to discern the true structure. At first glance it looks at times as if the short necks of the epidermal haustoria give rise to one or more branches which develop into haustoria. The deception arises from the crowded position of the organs.

On the under side of the leaf the epidermal cells are likewise penetrated by the slender tubes, some of which immediately enlarge into haustoria, and some of them (a little less than half), penetrate into the mesophyll cells immediately under the

epidermal cells. *Figs. 22–26* all represent cells on the under side of the leaves. The upper epidermal cells of the willow leaves in autumn are so filled with deeply staining products as to make the cells of this epidermis unfavorable for study.

As far as they have been observed the haustoria of *Uncinula Salicis* are not occasionally septate as in *Erysiphe communis*. In the possession of a single nucleus, surrounded by spongy protoplasm, and in its general shape, the haustoria of Uncinula are not peculiar. The subepidermal haustoria are also surrounded by sheaths such as *Erysiphe communis* has. But in the epidermal cells the sheaths are very frequently absent. The explanation of this absence of sheaths lies in the fact that Uncinula is capable of greater enzymic activity than Erysiphe, so that the sheaths are dissolved away. But by the time the tube has penetrated a palisade cell its supply of ferment is either exhausted or weakened (or both), so that the sheaths remain. The typical collar may sometimes be seen around the necks of the haustoria (*fig. 23*), but for the subepidermal haustoria it can be demonstrated at times, from the size and reaction to stains, that the penetrating tube is accompanied entirely across the epidermal cell by the cellulose ingrowth from the outer wall (*figs. 22, 24*).

De Bary does not mention the fact that the lobed appressorium of Uncinula may give rise to several haustoria (*figs. 22, 24*). Other appressoria, as far as they have been observed, produce absorbing organs singly, but on the willow leaf two or more tubes from the same appressorium pierce the epidermis close together. The confusion and crowding of haustoria in the cells is due to this fact, rather than to the fact that the extremely dense mycelium sends many single organs into the leaf. On the other hand, the lobed character of the appressoria seems to be produced by the contortion of the filaments necessitated by the origin of several haustoria in one place. The significance of the term appressoria consists in the fact that the expansions of the filaments which rise to haustoria are commonly closely appressed to the surface. But this habit is not uniform in *Uncinula Salicis*. *Figs. 23*, *25*, and *26* show that the appressoria may stand at some

distance from the surface of the host, and the penetrating tubes may have a shorter or longer course before they pierce the cells. Whether such appressoria have been forced away from the surface of the leaves by the resistance offered to the elongating penetrating tubes by the epidermis is not known.

It might be supposed that, where an intercellular space occurs between two subepidermal cells, the penetrating tube might find its way into the interior of the leaf. The haustoria of Uncinula, however, have not been found deeper than the subepidermal cells.

PHYLLACTINIA.

Palla (**24**, p. 68) has recently reported that Phyllactinia[6] has the very interesting habit of sending nutrient hyphæ through the stomata into the intercellular spaces of the infested leaves. Haustoria are thus constructed entirely on the interior of the leaf[7] and are not found in the epidermal cells as in Erysiphe. Because of this unusual habit Palla suggests the separation of the powdery-mildews into two families, the Erysipheæ and the Phyllactineæ. Upon the ground of certain differences, chiefly in the appendages of the perithecia, he gives (p. 65) the name *P. Berberidis* to the fungus on Berberis, as contrasted with *P. suffulta* on leaves of *Corylus Avellana*. No effort has been made to compare the material collected for this investigation with Palla's results for systematic purposes, but the writer can confirm most of Palla's observations on the intercellular hyphæ and haustoria. Palla finds that the haustoria on the intercellular hyphæ are found in the mesophyll cells in the two hosts he examined. As shown from a study of several hosts, Corylus,

[6] It seems worthy of mention that, on mature perithecia, the appendages in this genus do not extend parallel to the surface of the leaf, as in the young stages, but obliquely downward. The result is that the perithecia are raised into the air for the length of the appendages. The perithecia, therefore, fall off easily when the leaves are handled. It may be that the appendages serve the fungus as organs of distribution.

[7] Investigators who have thought of the Erysipheæ as purely epiphytic parasites, or as receiving their nutriment entirely from the epidermal cells, have been cited on p. 172. See also **27, 29, 31.**

Fraxinus, Cratægus, and Kornus, haustoria pierce the cells of the loose parenchyma in a minority of cases. Usually the intercellular hyphæ first penetrate the leaf to a region intimately associated with the fibro-vascular bundles (*fig. 31*) before producing absorbing organs. Sometimes haustoria are found in the cells between the bundles and the palisade cells, and sometimes in the palisade cells themselves. Palla observed hyphæ passing into the palisade layer, but he did not find haustoria there. In Xanthoxylum, however, haustoria frequently penetrate the cells of the loose parenchyma (*fig. 27.*) *Fig. 32* shows that the intercellular hyphæ which enter the stomata are either side branches of exterior hyphæ or the ends of original hyphæ. Except when the interior hyphæ arise as side branches immediately over the stomata, it is impossible to determine whether we have to do with an original germinating tube or not, so long as cross sections of leaves are used. If the stoma stands wide open, the initial cell of the penetrating hypha is not narrowed (*figs. 27, 28*), but upon the closing of the stoma the initial cell accommodates itself to the space left to it. It thus is narrow at the middle and becomes larger at the distal end (*figs. 30, 33*). Palla finds that the intercellular hyphæ of *P. suffulta* contain at most three cells (**24**, p. 7), and of *P. Berberidis* two (seldom three) more. The cells of the hyphæ within the leaves examined by me vary with the distance to be traveled before the production of an absorbing organ. Fewer than two cells were not found. The number is typically three to five. The distal cell of the intercellular hyphæ is sometimes extremely long. It is possible that, in tracing the sinuosities of the hyphæ through several sections, septa and nuclei may have been overlooked which would raise the number of cells to more than five. When the hyphæ produce their absorbing organs near the stomata, such hyphæ are noticeably larger than the surface hyphæ. But when the filaments extend a long distance through the intercellular spaces, some or all of the cells are more or less attenuated (particularly the distal cells.) An intercellular hypha may sometimes extend through more than a dozen sections. Haustoria do not appear

at the sides of the hyphæ exclusively, as Palla observed (**24**, p. 70), but frequently from the end, as in *figs. 29, 31*. In all of the hosts mentioned, excepting Xanthoxylum, the haustoria agree in structure with those of *E. communis*. *Fig. 31* shows the haustorium in one of the big parenchyma cells which form a sheath for the bundle. It also arises from the end of a hypha and contains a crystal which is so large as to distort the absorbing organ.

The haustoria of Phyllactinia on *Xanthoxylum Americanum* offer some striking differences in comparison with the ones just described. The intercellular hyphæ have thicker walls and the intercellular appressoria are conspicuous, flattened, sucker-like structures appressed tightly to the cells of the leaf (*fig. 28*). The leaves of Xanthoxylum have a thin layer of loose parenchyma. The bundles are near the lower epidermis. These facts of structure seem to influence the parasite. Its intercellular hyphæ, as a rule, are short and the cells are thick. They are more vigorous in appearance, the walls are less delicate, and they stain more readily than the surface hyphæ. Since the leaves of the host are thin the intercellular hyphæ are shorter than in those hosts where the haustoria are developed far from the stomata. No appressoria were observed on the surface hyphæ, though no special effort was made to find them. The appressoria of the intercellular hyphæ are numerous and conspicuous. Even beyond the point where the haustorium is produced, the hypha may adhere to the cell (*fig. 27*). The chief point of interest, however, is the absence of typical haustoria. In a long search through many sections I was unable to identify surely a single absorbing organ having the typical structure for haustoria of the Erysipheæ. There are numerous absorbing organs such as are represented by *figs. 27* and *29*. The penetrating tubes which pierce the host-cells are as minute as in Erysiphe, but the vesicles within the cells appear to have no protoplasmic contents. They have thick shining walls which, in exactly longitudinal sections, appear to be continuous with the walls of the host-cells. It was supposed at first that they were young haustoria differing

in the details of their development from the haustoria of Erysiphe; but their abundance and the many weeks for which the prickly-ash bush must have been infested when the material was gathered, make it evident that they are modified haustoria. It is to be seen that there is some resemblance between *figs. 27* and *29* and the early stages of penetration represented in *figs. 2* and *3* from Erysiphe. The haustoria of the fungus on Xanthoxylum certainly answer very well to the knob-shaped structures De Bary described, which were probably young haustoria. It is impossible to decide absolutely that they were, however, because of their similarity to *figs. 27* and *29*. Certainly if they represent dead haustoria, as De Bary thought, the vigorous mycelium must be nourished in some other way.

GENERAL CONSIDERATIONS.

The phenomena exhibited by the intercellular hyphæ of Phyllactinia are interesting in connection with what has been ascertained by several investigators in relation to the nutrition of fungi. It has been mentioned that the majority of the intercellular hyphæ in several of the hosts studied (excepting Xanthoxylum) take a more or less direct course to the regions near the bundles. The development by the fungus of the absorbing organs in regions abundantly supplied with available food, such as the parenchyma sheath of the bundles, indicates a selective chemotropism in the fungus. A selective chemotropism was reported by Miyoshi for several fungi in his paper already cited. Phyllactinia thus offers under normal conditions of growth a demonstration of the selective reaction which Miyoshi demonstrated by artificial means. This reaction enables Phyllactinia not only to surround itself with conditions which will insure it an uninterrupted supply of food and water such as is not insured to it while living as a purely epiphytic parasite, but also it is able to select within the leaf of the host those regions better supplied with food and water than the loose parenchyma. If the fungus is stimulated to place haustoria in cells joining the bundles to the palisade layer, or if haustoria enter the

palisade cells, they are still at the very source of that supply of food by which the plant maintains its vigor and activity. The proportion of cases to be found in which the intercellular hyphæ do develop haustoria in these more favorable regions is larger than casual observation would lead one to think. By a study of the cells of the host-leaf in sections preceding and following the section which contains the haustorium, it may often be determined that the fungus actually has placed its absorbing organs in one of the favorable cells. It should not be thought, however, that this is done invariably. In Xanthoxylum the leaves are so constructed that the bundles are near the lower epidermis through the stomata of which the fungus finds access. All of the mesophyll cells, therefore, have a surplus of food. This fact would account for the number of mesophyll cells which contain haustoria.

If it be demonstrated that the mildew on Xanthoxylum does not possess typical haustoria under any conditions, it will be important to discover whether the apparently stunted haustoria can absorb food for the fungus as well as typical organs. If they are not effective, how far is the fungus nourished by saprophytic methods? In the first place, the intercellular spaces of the leaves of this particular host are abundantly supplied with organic material. On the part of the parasite itself it is noticeable that, when under the stomata, the intercellular hyphæ encounter parenchyma cells which block the way, the cells of the hyphæ are short, thick, and vigorous; not only when the haustoria are produced near, but also when the hyphæ have haustoria at some distance from the stomata. But the hyphæ which do not encounter such cells, but run a comparatively uninterrupted course before constructing haustoria, are more or less attenuated and are less vigorous in appearance. If some cell of the hypha in such a case lies in contact with a parenchyma cell (*fig. 33*, penultimate cell), that cell of the hypha is short, thick, and vigorous. Büsgen's results would seem to show that Erysiphe does not succeed as a saprophyte. At least, he found that its germinating tubes had a limited growth under the conditions

he was able to establish. He did not succeed in infecting pieces of leaves arranged for the purpose. If, under natural conditions of infection, the germinating tubes have a limited growth unless supplied with nutrient material from the host in some way, it is not clear how they can obtain it so as to grow down into the leaves for comparatively long distances, as Phyllactinia does, before producing haustoria, unless the fungus appropriates intercellular material. The subject is still open for investigation. It is possible, of course, that the first side branch, passing into the interior of the leaf, places an absorbing organ near the stoma and thus supports the whole branching system until other side branches in other stomata are able to assist.

There is some evidence to support the possibility of intercellular nutrition in this fungus, as has been established for others by Nordhausen, Ward, Büsgen, and Frank. This investigation, however, has not embraced the question of how far, if at all, the abundant intercellular material in Xanthoxylum leaves is available, though some facts were observed which suggest the possibility of intercellular nutrition of the parasite which have not been observed in other hosts infested by Phyllactinia.

There are two points connected with my observation of Erysiphe on the geranium leaf which may be mentioned briefly. At the end of a section where the scissors with which the pieces of leaves were cut had destroyed the section in part, a haustorium was found in what was clearly a subepidermal cell. Its connection with the surface was destroyed, but there is no doubt that it was a normal haustorium in one of these cells. Whether it was due to the chance presence of Phyllactinia on this host, whether Erysiphe occasionally adopts the practice of *Uncinula Salicis*, or whether it was Uncinula itself on this host, could not be determined. With this circumstance is related a note on page 9 of Ellis and Everhart's *Pyrenomycetes*. This note corrected the mistake of the artist (F. W. Anderson) who, it was supposed, wrongly represented (*fig. 3, pl. 1*) a germinating tube from a conidium of *Sphaerotheca Castagnei* as entering a stoma. My observations render it probable that the artist saw what he

represented, though it may have been a tube of Phyllactinia. Whether or not Sphærotheca has a similar habit to Uncinula, I have not determined.

It is a pleasure to acknowledge the assistance I have had in this investigation from Professor C. R. Barnes, under whom the work was begun, and from Professor R. A. Harper, under whom it was mainly accomplished.

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LIST OF GENERA AND SPECIES STUDIED.

Erysiphe communis (Wallr.) on *Geranium maculatum* L.
——— *graminis* DC. on *Poa pratensis* L.
——— *Galeopsidis* DC. on *Scutellaria lateriflora* L.
——— *Galeopsidis* DC. on *Galeopsis Tetrahit* L.
——— *communis* on *Polygonum aviculare* L.
——— *Cichoracearum* DC. on *Eupatorium perfoliatum* L.
Sphærotheca Castagnei Lév. on *Bidens cernua* L.
Podosphæra Oxycanthæ DC. on *Prunus* sp.
Microsphæra Russellii Clinton on *Oxalis corniculata stricta* Sav.
Uncinula Salicis DC. Wint. on *Salix discolor* Muhl.
——— *necator* Schw. on *Vitis* sp.?
——— *Clintonii* Peck, on *Tilia Americana* L.
Phyllactinia suffulta (Reb.)[1] on *Fraxinus pubescens* Lam.; *Cratægus punctata* Jacq.; *Xanthoxylum Americana* Mill; *Corylus Americanum* Walt; *Cornus stolonifera* Michx.

Such forms as are not discussed in the preceding pages have not been found to differ so materially from *Erysiphe communis* as to require a separate discussion of their haustoria.

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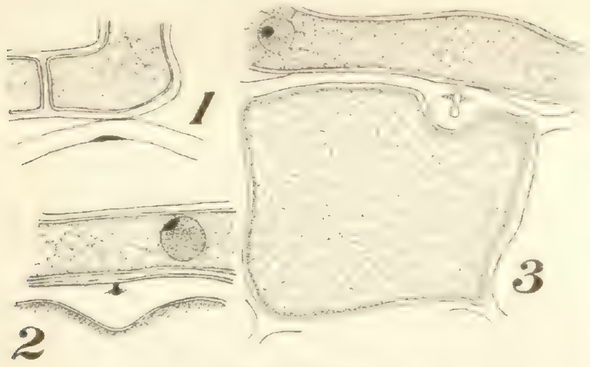
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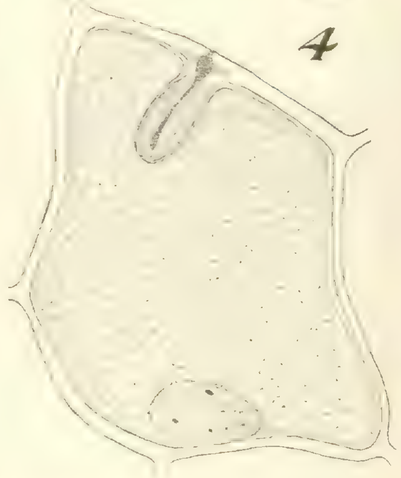

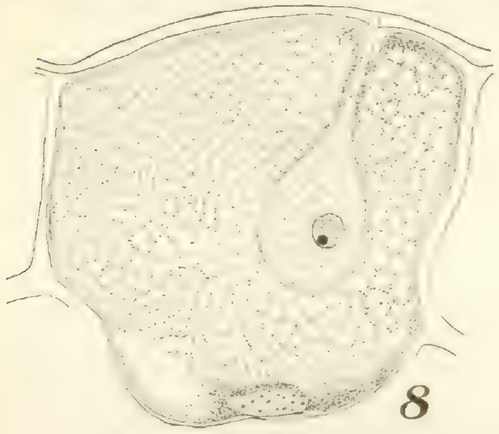
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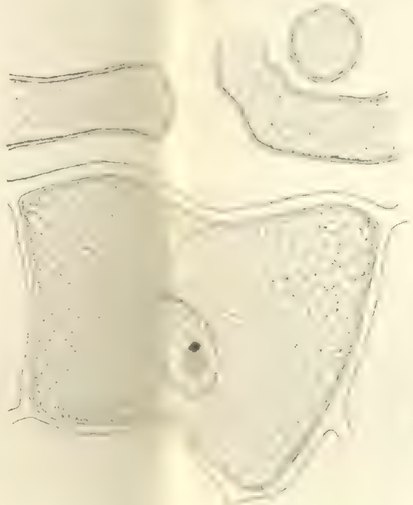
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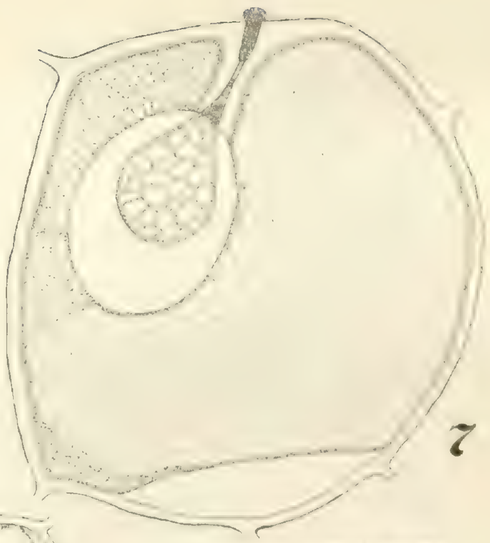
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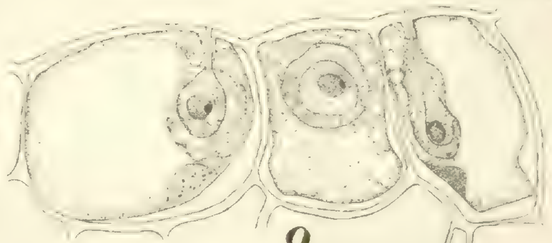
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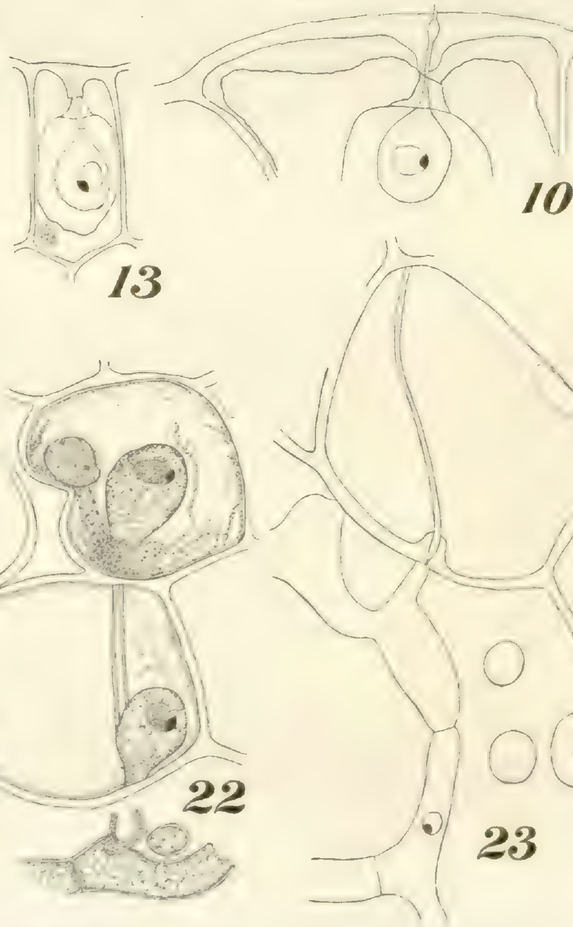
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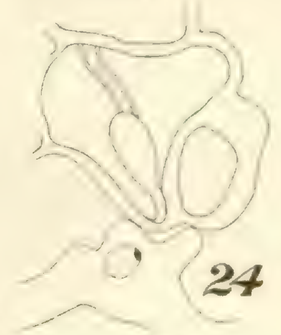
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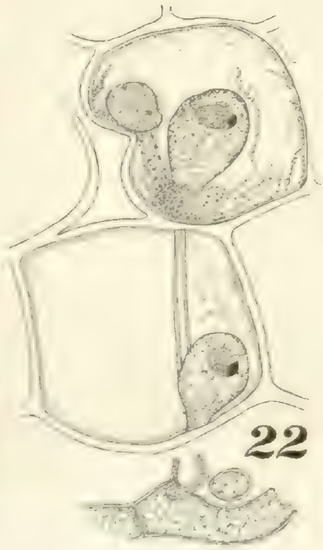
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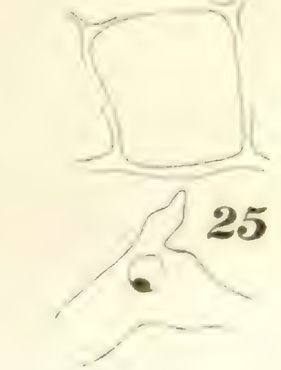
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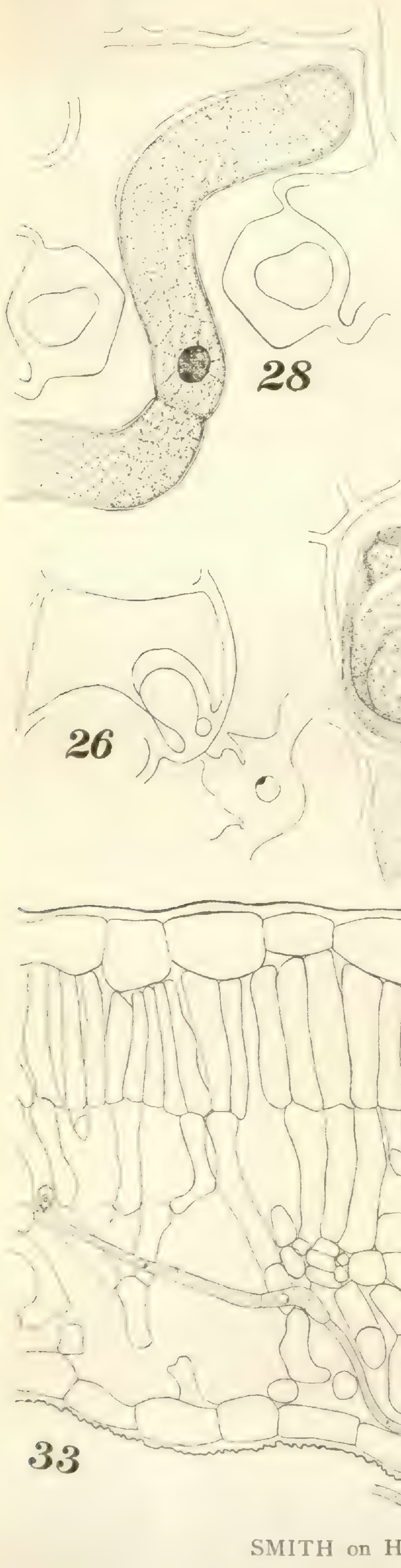

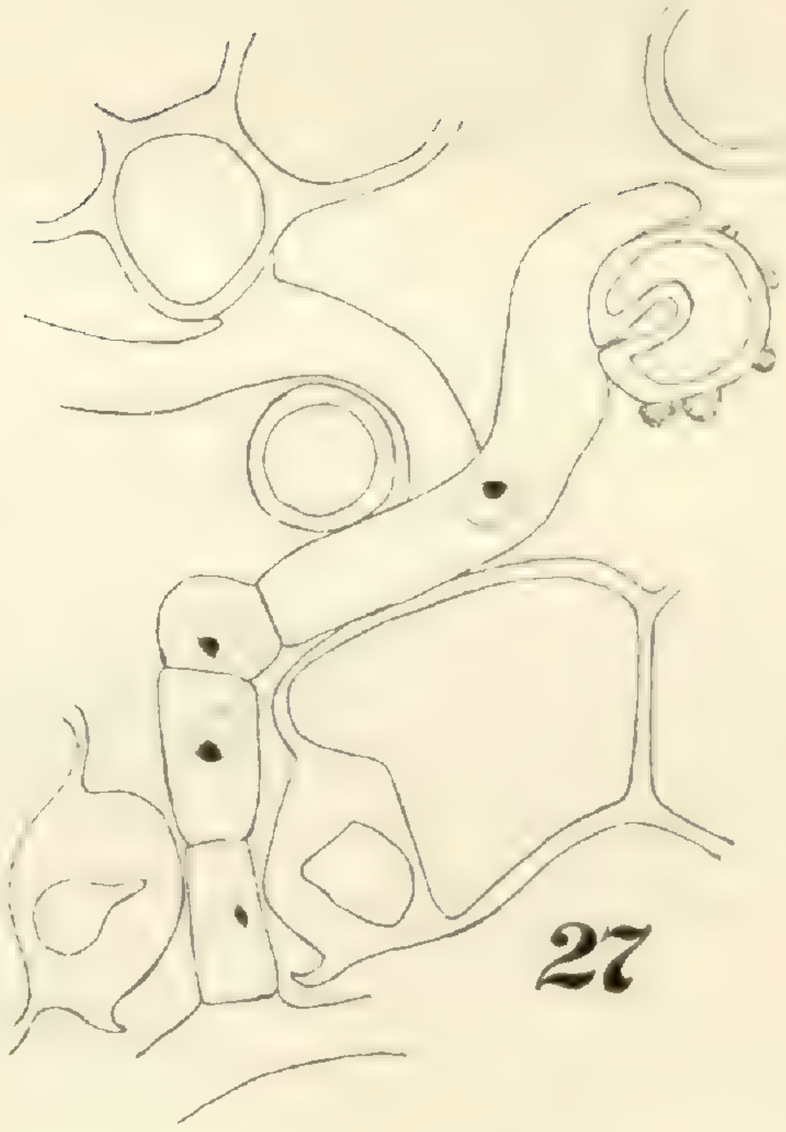

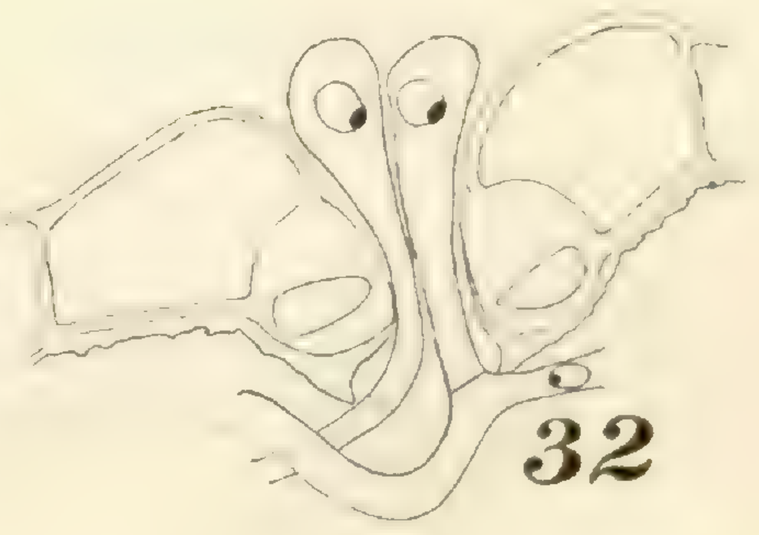

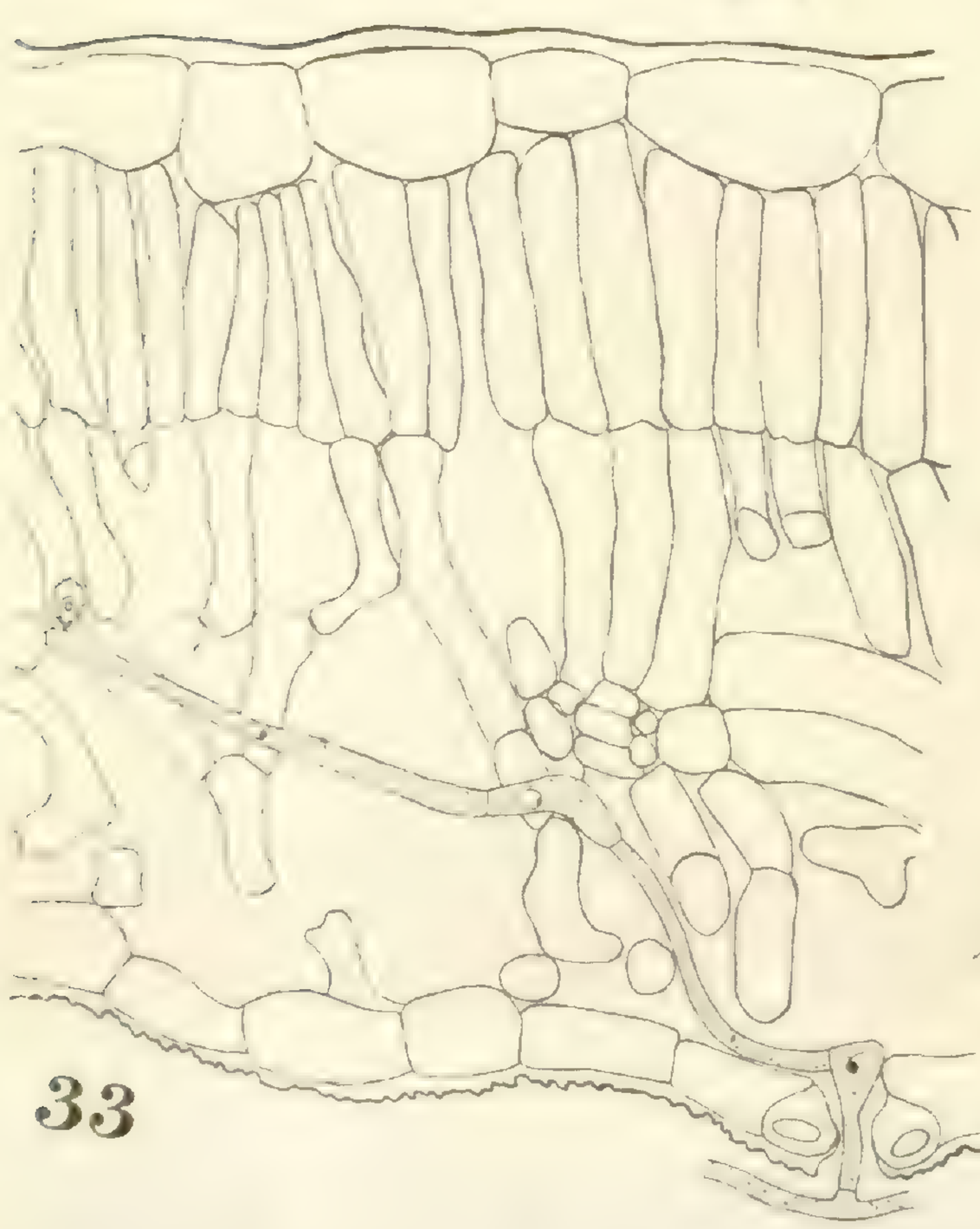

SMITH on HAUSTORIA OF ERYSIPHEÆ

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EXPLANATION OF PLATES XI AND XII.

All the figures were drawn by the aid of the Abbé camera.

Magnification of *figs. 9, 11, 13, 22 to 30*, 900 diameters; *figs. 16, 28*, 2000 diameters; *figs. 32, 33*, 400 diameters; all other figures, 1800 diameters.

FIGS. 1–15. *Erysiphe communis* on *Geranium maculatum.*

FIG. 1. First stage in penetration, marked by spot on inner surface of host wall.

FIG. 2. Penetrating tube just beginning to make its way through epidermal wall. Wall thickens as tube grows.

FIG. 3. Having enlarged at a point in line with the inner boundary of the epidermal wall the tube continues its growth.

FIG. 4. Further stage in penetration. Cellulose papilla elongates as the tube grows. Distal end of cellulose in growth begins to show signs of disintegration. Nucleus of host-cell on basal wall of cell.

FIG. 5. Distal end of penetrating tube now begins to enlarge. Cellulose further disorganized. The proximal end of ingrowth not disintegrating, but destined to remain as collar about neck of haustorium.

FIG. 6. Young haustorium escapes from cellulose thickening and is developing without sheath.

FIG. 7. Stage before entrance of haustorium nucleus. Stretched and intruded plasmic membrane of host-cell forms bounding membrane of sheath, which in this case is devoid of contents.

FIG. 8. Haustorium without sheath.

FIG. 9. Middle haustorium in optical section, the two at end in longitudinal section. Sheath present about haustoria.

FIG. 10. Plasmolyzed cell showing collar as an ingrowth of cellulose from cell wall. Partly in perspective.

FIG. 11. Haustorium with two nuclei. Septum also found across neck.

FIG. 12. Haustorium without sheath. Protoplasm of host-cell adherent to sides of neck.

FIG. 13. Haustorium shows septum across neck.

FIG. 14. Elongated nucleus in mycelial hypha.

FIG. 15. Membrane absent from sheath, which here consists of lumps of disintegrated cellulose adhering to body of haustorium.

FIGS. 16–17. *Erysiphe Cichoracearum* on *Eupatorium perfoliatum*.

FIG. 16. Basal cell of hair containing haustoria.

FIG. 17. Shows unstained area about point of penetration. Remainder of host wall staining darkly.

FIGS. 19–21. *Erysiphe graminis* on Poa. Three branching haustoria.

FIGS. 22–26. *Uncinula Salicis* on *Salix discolor*.

FIG. 22. Epidermal cell containing one haustorium, while from the same appressorium another penetrating tube passes through the epidermal cell into the subepidermal cell. The sheaths are not visible.

FIGS. 23–26. Various forms of appressoria giving rise to two or more haustoria.

FIG. 27. Modified haustorium arising from appressorium and penetrating mesophyll cell. Host-cell shows exudations on its exterior. A second appressorium also shown.

FIG. 28–33. *Phyllactinia suffulta; figs. 28, 31* on *Fraxinus pubescens; fig. 30* on *Cornus* sp.; *figs. 27, 29, 32, 33* on *Xanthoxylum Americanum*.

FIG. 28. Part of an intercellular hypha. Guard cells drawn apart and hypha not compressed, as in *figs. 32, 33*.

FIG. 29. Smaller haustorium, and arising from end of hypha. Exudation on cell of leaf shown.

FIG. 30. Intercellular hypha consisting of four cells. Haustorium arising from side of distal cell. Host-cell below palisade cells.

FIG. 31. Haustorium arising from end of intercellular hypha and penetrating parenchyma cell connected with bundle. Haustorium contains a crystal.

FIG. 32. Stoma containing initial cells of two intercellular hyphæ, one a side branch. Origin of the other is indeterminate.

FIG. 33. Intercellular hypha, with haustorium in cell joining bundle to palisade cell. Middle cell of hypha is short and thick, and lies on cells of host.

STUDIES ON THE GEOTROPISM OF STEMS.

EDWIN BINGHAM COPELAND.

1. The absence of polarity in the hypocotyl of Cucurbita.

THE hypocotyl of Cucurbita, and, I suppose, of every plant whose cotyledons expand and act as leaves, is negatively geotropic in its ultimate reaction. When the hypocotyl is in any other position than the vertical, the under half of it grows more rapidly than the upper. This is regarded as a response to the unusual disposition of the burden of the parts of the hypocotyl, as they rest upon one another; and the seat of perceptivity and response is more specifically located in the green cortex.[1] The purpose of the reaction is to get the cotyledons into the light, which, when the seed germinates in the ground, will be accomplished by pushing them upward. Now it is evident without argument that an excess of growth of the under half of the hypocotyl will place its upper end in a vertical position, so that its further growth will be upward only in case the basal end is fixed in its position and the naturally upper end is free—a condition which is fulfilled in nature by a considerable growth of the root before the elongation of the shoot commences.

Teleologically, perhaps phylogenetically, the geotropism of the shoot has been developed along lines of "lengthwise" propriety: *i. e.*, in order to secure a particular linear arrangement of root, hypocotyl, cotyledon, etc. But in the individual plant today, according to Czapek's explanation (*loc. cit.*), which is the only rational one I am acquainted with, the response is to a disturbance of the normal "crosswise" arrangement, so that each growing part of the hypocotyl acts without reference to the parts more or less remote from the cotyledons.

The question as to whether or not any trace of the development of geotropism remains in its manifestation in the present

[1] CZAPEK, F.: Weitere Beiträge zur Kenntniss geotropischen Reizbewegungen. Jahrb. f. wiss. Bot. **32**: 248. 1898.

plant has seemed to me worthy an experimental answer. Such a trace would appear as a sort of polarity, such that if the fixed point of the hypocotyl were moved upward from the base, only the upper free part would remain disposed to become erect. To answer this question I transferred the fixed point at once from base to apex, in each case leaving the other end free. The result was unequivocal, and as the data from several experiments were in all essentials alike, it will suffice if a single series is reported.

The seeds were germinated on a net over water and the seedlings selected were perfectly straight and as uniform as possible. The hypocotyls, 6–6.5^{cm} long, were marked off into zones of 1^{cm} each, and these zones were numbered from the cotyledons downward. The end to be fixed was imbedded in a block of gypsum plaster, and these blocks were placed, with the hypocotyl horizontal, in a closed glass vessel containing some water. The experiment was begun at 10 A.M., April 12, 1899, and at 4 P.M. the free ends were all directed upward at angles of 50–70°, those having free cotyledons being somewhat more sharply elevated than those having free roots. They were left undisturbed for six days, at a lower temperature than Cucurbita likes, about 18° C. in general, and were then removed and the growth and curvature measured. The curvature is expressed in the following table in figures representing the radius of the arc, measured by a Sachs' cyclometer. Plants 2 and 4 had the roots imbedded; plants 1 and 3 the cotyledons, so that zone I was next the plaster.

PLANT 1.

Hypocotyl straight and erect (the roots in air) to within 6^{mm} of the cotyledons. The radius of the curve for the upper 5^{mm} of the hypocotyl and the exposed 5^{mm} of the cotyledons was about 1^{cm}.

Zone	I	II	III	IV	V	VI
PLANT 2.						
Curvature (in cm.)	15	9	6	3	5	15
Growth (in mm.)	3	3.5	2.7	2		
PLANT 3.						
Curvature (in cm.)	2	3	4	7	12	
Growth (in mm.)	1.7	1.2	1.3	1		
PLANT 4.						
Curvature (in cm.)	14	10	4	3	4	8
Growth (in mm.)	1.5	2	1.7	1	1	1

The conclusion, which has been anticipated, is that the response to gravity of the horizontal hypocotyl is always the same, whether the result is beneficial or, under artificial conditions, detrimental. It is a response to local conditions in each individual zone of the hypocotyl, and is executed without the slightest regard to the *relative* positions of the different zones, or the serial parts of the plant, roots, hypocotyl, cotyledons.

The pumpkin has even, figuratively, no brains. Its response to a stimulus is blind, like the instincts of animals: merely an effect, devoid in any individual instance of a purpose. As is often at least true of instinct, the response is not directly to the condition it is designed to correct, or to suit, but to something correlative, or merely concomitant. In response to a shifting of the pressure upon one another of the transverse elements of a tissue, the plant executes a change in its growth, which becomes of some service only when it results in a certain longitudinal arrangement of the plant-members; this longitudinal arrangement is the thing at fault, but the plant cannot perceive it. In nature the response meets the hidden purpose, but under changed conditions the same response is made, and is fatal. Certain flies flock at the scent of carrion, not in reality to gratify their peculiar æsthetic sense, nor yet to get a meal, but because it takes them where their eggs will thrive; the Dictyophora panders to their instincts; the carrion flies revel in its slime, and, mistaking the attribute for the reality, deposit their eggs where they rot. The behavior of the pumpkin and the fly is essentially the same; both react blindly, but in nature, fortunately.

A careful inspection of the table given above will show, in the different location of the region of greatest curvature in the plants with encased roots and in those with encased cotyledons, a nice demonstration that each zone of the hypocotyl can act for itself. In the former the hypocotyl is somewhat curved throughout, even in the most mature basal part, and most so about 4^{cm} below the cotyledons, the upper, youngest part being almost straight; while when the cotyledons were encased the curvature

is most marked within 1^{cm} of them, and the older part is straight. This difference could not occur if each zone were not able both to be geotropically irritated, and to respond to the irritation. If the experiments lasted several days it was found that the stems which were fixed at the apex were usually more curved than those fixed normally, at the base, so that in this case the end in the air was carried well beyond the vertical position. This was obviously because the youngest part remained horizontal, and as the older part matured with more or less curve the part still growing kept bending itself upright, and so carried the older part beyond the vertical.

The hypocotyls of *Helianthus annuus* and *Lupinus albus* and the epicotyls of *Pisum sativum* and *Phaseolus vulgaris* were tested, but showed no behavior different from that of Cucurbita, so that it is not worth while to encumber this paper with the individual results. The nutation of Phaseolus caused some queer curves, and the same would probably be found the case with Cucurbita when the epicotyl changes from orthotropic to plagiotropic. The behavior in response to stimulation by light is analogous. No experiments were undertaken especially to show this; but when seeds of Lupinus were germinated in holes in a floating cork in a glass vessel, and grew so that the cotyledons kept their place while the hypocotyls extended downward into the water, the latter became concave on the light side, and the roots were carried toward the window.

Any indication of real polarity is likewise wanting in roots. This is not easily demonstrated, as the curvature is largely executed in the roots of the plants I have been using, within 1.5–2^{mm} of the tip, and it is difficult to imbed them so that the tip will stay fast without encasing the part which should be free to react. Nevertheless, I have succeeded occasionally with the roots of Cucurbita, Lupinus, Helianthus, and Pisum, and in every case the result was an excess of growth of the upper side of the root, by which the shoot end of the plant was carried downward. This went as far as about 90°, but I have hitherto been unable to make the tip stay imbedded while the free end is bent

around indefinitely, as F. Darwin[2] did with the cotyledons of Sorghum.

2. The geotropism of split stems.

While it is certain that every growing part of the stem can perceive the geotropic stimulus and execute the response *in loco* it is not impossible that if the local perceptivity could be interfered with, a growing zone might respond to a stimulus transmitted to it from another part of the plant. My first experiments with split hypocotyls were with a view to answering the question; but they were not appropriate, because, as Sachs[3] showed, and as anybody can easily demonstrate, a half stem is in itself irritable. The results which they did yield, however, were surprising enough.

Cucurbita.—The first experiments were on Cucurbita hypocotyls, partly or wholly split, the split being either transverse or parallel to the plane of the cotyledons. Of three similar experiments it will suffice to report the following one, which began May 24, and lasted forty-eight hours. The growth is reported, and the angle made by the free end with its original horizontal position.

	Growth in mm	Curvature in degrees
1 Free	40	80
2 Split vertical	8	75
3 Split vertical	4	70
4 Split horizontal	13	110
5 Split horizontal	18	180
6 Split horizontal	10	165
7 Split horizontal	5	180

No. 1 was fastened in place without imbedding; nos. 5 and 6 had the cotyledons imbedded; and the others, the roots. The

[2] F. Darwin, in "Botany at the British Association," Nature **61**: 67. Nov. 16. 1899. After other evidence that geotropic perceptivity is localized in the cotyledon while the hypocotyl executes the response, he says: "If the seedling is supported by its cotyledon (which is fixed in a horizontal position) while the hypocotyl projects freely . . . . the hypocotyl begins to curve upward . . . and it does not cease to curve when the free end points vertically upward; the curvature continues indefinitely, so that the hypocotyl curls into a spiral of three or four rings."

[3] Sachs: Ueber Wachsthum und Geotropismus aufrechter Stengel. Gesammelte Abhandlungen **2**: 969. 1893. In the experiment Sachs reports, the growth of the lower half did not overcome the tissue tensions.

depressed growth of nos. 2 and 7 is correlative with the imbedding, as well as due to the wound. Removing the plumule does not hinder the elongation of the hypocotyl. When the split was horizontal the halves became bowed apart, and the angle of curvature given is the least at which they could be brought into continuous contact.

The first notion suggested by the excessive curvature of the hypocotyls with horizontal split surface is that they are responding to a stimulus received by the imbedded part of the plant. But the facts that a half stem is known to be in itself irritable, and that the extreme curvature, 180°, occurred whether it was root or cotyledon that remained horizontal, point toward the conclusion that in the experiment each half of the split hypocotyl responds only to a stimulus received *in loco*; and that a half hypocotyl has something in its own structure, independent of any comparison of conditions with the other half, which will make it grow more rapidly if the split is the upper than if it is the lower surface.

Two plants were next split from the tops well into the roots, one having the cotyledons split, the other separated; both had the roots imbedded. The halves of one were too weak to become quite erect, but those of the other bent up side by side, and after they became erect the lower half slid along the upper so as to reach beyond it. In both cases the growth of the lower half exceeded that of the upper by 3^{mm}. The experiment was repeated, giving a little less difference.

July 13, a number of plants were split from end to end, and the entirely separated halves imbedded side by side, some with the roots, others with the cotyledons free, all with the cut surface horizontal. The growth in forty-eight hours follows:

	Growth of upper half in mm	Growth of lower half in mm
1.	2.5	3.5
2.	2.0	3.5
3.	2.5	4.0
4.	3.5	5.0
5.	2.0	2.3
6.	3.0	4.0

In every instance the lower half grew more than the upper.

July 14 the experiment was repeated with older plants. The average growth of nine plants in forty-eight hours was: in the upper half, 1.5^{mm}; in the lower half, 2.2^{mm}. In every instance except one the greater growth was made by the lower half. It occasionally chanced that one half twisted into the other's position, which caused the difference to be wanting or less marked.

Later in the year in connection with work on other plants, I put five split plants into glass tubes too small to let them bend. The average growth of the lower halves in three days was 26^{mm}; of the upper halves, 16^{mm}. At the same time I made a small attempt to see what is the rate of growth of a horizontal half stem in either position as compared to one in its natural erect position. Three plants were split throughout, and one half of each was put into an upright glass tube. In three days the average growth was 4.8^{mm}. The other halves were put into horizontal tubes, with their split surfaces up, and grew in the same time on an average 14.3^{mm}. Of three other plants the average growth of the erect halves was 24^{mm}, and of the horizontal halves with split surface down, 24.3^{mm}; but two of these latter had twisted so that part of their growth was made with the cut surface up. The comparative growth of erect and horizontal halves was more fully experimented on with Lupinus.

Phaseolus vulgaris. Three epicotyls, 4–5^{mm} in length, were split November 3, and the cotyledons were imbedded so that the split surfaces were horizontal. In three days the average growth of the upper halves was 3.2^{mm}; of the lower, 5.7^{mm}. The curves necessary to bring the halves together were 95–145°. November 20, six epicotyls were split, and the halves fastened in the same positions with glass needles. In two days the average growth of the upper halves was 25^{mm}; of the lower, 27.2^{mm}. Small as the average difference is, the lower half was longer in every instance.

Caladium sp. On large corms that had been brought into the greenhouse for the winter the stubs of the shoots were still growing slowly. These stubs were made up of some very young

leaves in the middle, surrounded by the fleshy petioles of the leaves the rest of which had been removed. Two of these petiole stubs were present, each reaching around far enough so that its edges lapped over one another. These petioles should execute any curving that occurs. I cut the end of the stub off square, and then split it into several slices, in such a plane that the upper and lower parts of the larger outer cotyledon were symmetrical, and placed the corms so that the split surfaces were horizontal. The atmosphere was unfortunately not saturated, and cutting and splitting the fleshy parenchyma gave such an opportunity for evaporation that in most cases after a week a shortening instead of an elongation had occurred. Nevertheless, a slight upward curve of each slice was noticeable, and a difference in their growth could be detected in spite of the shrinking. The following two experiments may represent the five made:

1. Diameter of stub, 3mm. Cut into four equally thick slices. Change in length of outer petiole in six days:

1st (undermost) slice.		no change
2d	"	—1 mm
3d	"	—1.3mm
4th	"	—2 mm

2. Diameter 35mm: in five slices. Change in six days:

1st (undermost) slice.		+1 mm
2d	"	—0.4mm
3d	"	—0.6mm
4th	"	—1.0mm
5th	"	—2.0mm

It appears then that where these composite stem structures are split into a series of slices the growth of these is successively less from below upward. Some of these slices consisted (aside from the epidermis) entirely of the large celled cortical parenchyma, and seemed able individually to execute geotropic curvatures. Caladium is the only subject with which I have succeeded in getting a series of longitudinal slices of sufficiently equal thickness to give any kind of results.

Helianthus. Nine hypocotyls of the "mammoth Russian" variety were split, the cotyledons being either separated or split, and the split extending 1cm into the root. They were placed in horizontal glass tubes. After a day, four plants in which the difference in the growth of the halves was well marked were turned over, so that the halves exchanged places.

	December 5. Length in mm.	December 6. Growth in mm. Lower half.	Upper half.	December 8 — Growth from December 5. in mm. Former lower half.	Former upper half.
1.	17	6	3	8	6
2.	30	8	5	15	26
3.	27	8	6	13	26
4.	25	8	4	16	15
5.	26	8.5	5		
6.	13	9	8		
7.	26	6	5		
8.	15	6	5		
9.	35	18	16		

The average growth of the under halves of the first four during the first day was 7.5 mm: during the following two days, when they were the upper halves, their average was only 5.5 mm. The average of the upper halves changed at the same time from 4.5 mm to 13.75 mm. There is no possibility of error either from unequal splitting or individual variability in these results.

Lupinus albus. The large, straight, solid hypocotyls of Lupinus are the finest subjects I have found for these experiments, and have been very freely used. November 15 four plants were split throughout, and imbedded at either end. After three days the average growth of the upper halves was 4.25 mm; of the lower halves, 10.5 mm. The lower half was always the more curved, in spite of the tissue tensions which at first bent it downward. It was indifferent whether the cotyledons were split or separated. Of a number of plants started November 17, and marked into 1 cm zones, the following two were interesting in their behavior. Both twisted so that the halves changed positions. After three days the growth of each half of one of them was 14 mm: at first the lower half gained (as was shown by measuring the individual zones), and then after their positions were reversed the other caught up. The upper and lower halves of the other plant grew respectively 15 mm and 13 mm, but before they changed places the lower was 2 mm ahead. Of six plants split and put into glass tubes, November 28, so that they might grow in length but could not curve, the average excess in length of the lower half after two days was 5 mm. Of seven plants

treated in the same way December 1, the average growth of the upper half in two days was 4.4^{mm}; of the lower, 9.1^{mm}. Of thirteen plants split 1^{cm} into the root and placed in horizontal tubing, the average growth of the upper halves in two days was 2.4^{mm}, and of the lower halves, 4.4^{mm}. Three plants were turned over; and after two more days the halves of two of them were equal, but in the other the difference had increased.

It has now been shown for hypocotyls and epicotyls, hollow and solid stems, fixed at either end by imbedding in gypsum plaster or pinning with glass pins, or grown in glass tubes, that the rate of growth of an isolated half stem is greater, in general perhaps twice as great, if it occupies the position of the inferior half of an uninjured prostrate stem, than if it is in the position of the superior half. As to the fact, the proof is surely sufficient. But so far no explanation has suggested itself, which was not more easily confuted than conceived.

After looking in vain for a real reason, I turned to the mechanism of the growth, but have been unable in a considerable number of experiments to detect any well marked or constant difference in turgor between the halves. If the turgor of the growing region at a fixed distance below the insertion of the cotyledons is determined it will be found less in the upper half, but this is because the growing region is shortened. If the zone which is elongating most rapidly is tested in each case (this will be perhaps 2^{mm} nearer the base in the under half) there will be found almost no difference in the turgor. The results from testing a number of plants were very constant, and the following may serve as an example. The halves had been horizontal for four days. Turgor is measured in percentage concentration of KNO_3 necessary to begin plasmolysis.

Lupinus albus.

Growth		Upper half 7^{mm}		Lower half 15^{mm}	
		Growing part	Grown part	Growing part	Grown part
Turgor	Pith	4	3	4	3·5
	Cortex	4	3–3·5	4	3–3·5

Ceteris paribus, however, the more rapid growth of the lower half would depress its turgor,[4] so that the equality observed indicates that with equal growth the lower half would have its turgor raised. It was noticeable that in general the relation of turgor in pith and cortex was the same in both halves (as in the growing part, in the figures just given); although to bring a pressure to bear against the tube which kept them straight, one half should manifest an excess of turgor in the cortex, the other rather in the pith. I do not know whether or not the entire stems would show any difference in the turgor of the halves, such as Pfeffer[5] observed in some grass nodes; but they do exert an upward pressure by the elimination by growth of the tension between the walls and cell-sap of the under side, so that the osmotic pressure is available for outside work. If a hypocotyl of Lupinus be removed from a horizontal glass tube and immediately split, the lower half stretches out, often at least 2^{mm} longer than the upper, and this difference is maintained after entire plasmolysis.

To determine the effect of the position of the horizontal half-stems on the rate of growth, as compared with the normal upright position, I paired a number of plants, split them, matched the halves of each plant with those of the other plant of the same pair, put them into glass tubes, and placed one tube erect, the other horizontal. Then one half of *A* and one half of *B* were erect; the other half of *A* was horizontal with the split surface up, and the other half of *B* was horizontal with the split surface down. They were wrapped in moist filter paper, and except for their position with regard to gravity were under as like conditions as could be desired. Of a series of six plants treated in this way, the growth of the erect halves in two days averaged 7^{mm}. The growth of the horizontal halves, whose cut surface was downward averaged 6.8^{mm}. At the same time the complementary six plants averaged: the erect halves, 8.1^{mm}, and the horizontal halves, with split surface up, 17.1^{mm}. Dec. 8, ten

[4] COPELAND: Ueber den Einfluss von Licht und Temperatur auf den Turgor. Inaug.-Diss. Halle a. S. 1896.

[5] PFEFFER: Druck und Arbeitsleistung durch wachsende Pflanzen.

pairs of plants were treated in the same manner. In three days the average growth was:

Of ten erect halves - - - - - - - -	15.7mm
Of corresponding horizontal halves, split surface down -	13.9mm
Of other ten erect halves - - - - - -	12.8mm
Of horizontal halves, split surface up - - - -	22.9mm

Or, calling the growth of the erect halves 100, that of the horizontal halves with split down was 88.5; that of horizontal halves with split up, 178.9.

The growth of the isolated under half then is decidedly accelerated, while that of the upper half is in a lesser measure retarded. Sachs[6] long ago showed that this happens when an entire stem executes its response to geotropism, and it is interesting to note that isolation of the halves does not affect the quality of the reaction at all. This ought to give the quietus to all of the various theories which would explain the execution of the geotropic response by processes taking place entirely in either half.

The behavior of split stems emphasizes the fact that geotropic irritability is dependent upon the relative positions of the tissues of the stem: and seems to me to point toward a more intimate connection of the perception of the stimulus with the execution of the response than we have hitherto felt justified in assuming. The execution of the response by whole stems does not demonstrate any transverse transmission of a stimulus by which the halves compare their positions, for the behavior of the separate halves shows that no comparison is required.

UNIVERSITY OF WEST VIRGINIA,
Morgantown.

[6] SACHS: Längenwachsthum der Ober- und Unterseite horizontal gelegter sich aufwärts krummender Sprosse. Gesammelte Abhandlungen 2: 945. (From Arb. des botan. Inst. zu Würzburg 1: 193. 1872). On p. 955 he says: "Bei der Aufwärtskrümmung eines frei horizontal gelegten Sprosses wächst von je zwei gleichnamigen Gewebestreifen immer der der unteren, konvexen Seite stärkes, der der oberen, konkaven Seite schwächer als die gleichnamigen Gewebestreifen eines aufrechten Sprosses in derselben Zeit."

BRIEFER ARTICLES.

THE NUTATION OF HELIANTHUS.[1]

In a former contribution[2] the writer presented the results of extended observations on the nutation of the wild variety of *Helianthus annuus*. Considerable subsequent study in the same direction has fully confirmed the statements made at that time. It was, however, impossible to present satisfactory illustrations of the plants in the field, no camera being at hand when the observations were made. Since there seems to be some skepticism as to the fact of nutation, it was thought desirable to add a few more recent studies and some photographs showing the actual appearance of the plants in the field.

Fig. 1.—Cultivated *Helianthus annuus* at 6 P.M., three plants showing the westward nutation, and two with the heads tipped to the east.

During the summer of 1898 a series of observations was made in Columbus, O., on the common cultivated variety. The cultivated sunflower behaves very much like the wild one, except perhaps that it appears somewhat less striking in its reactions. The growing plants nutate from 60° to 90° west in the evening (*figs. 1, 2*), and from 50° to 70° or more, east in the morning (*fig. 3*). At night the leaves droop and the tips point downward.

When anthesis begins nutation ceases and the heads are tilted toward the east or northeast (*fig. 4*). Not only the main terminal heads but also some of those on the side branches take this position.

[1] Contributions from the Botanical Laboratory, Ohio State University. VII.

[2] Observations on the nutation of Helianthus annuus. Bot. Gaz. **25**: 395–403.

The effect is most striking, however, in the case of plants with a single large head. It was observed that plants growing on the south

FIG. 2.—Cultivated *H. annuus* just before sunset, showing westward nutation.

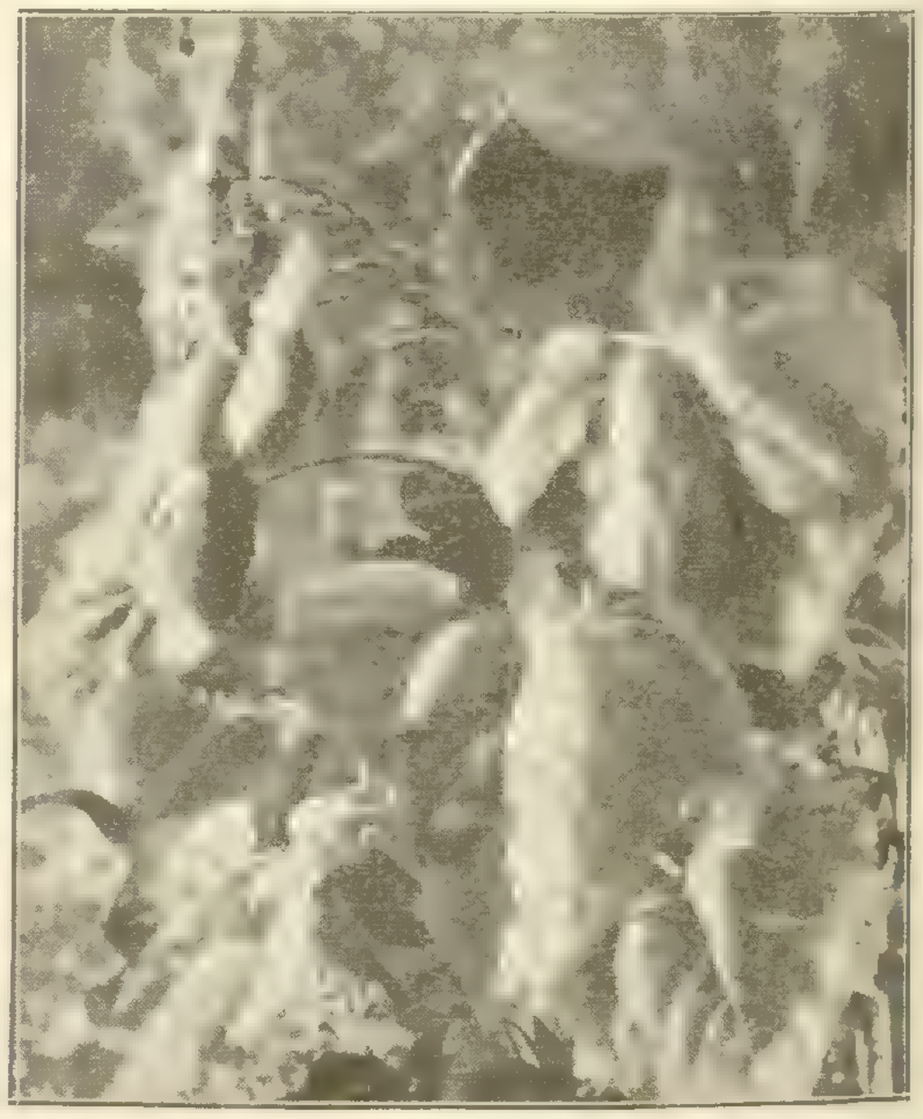
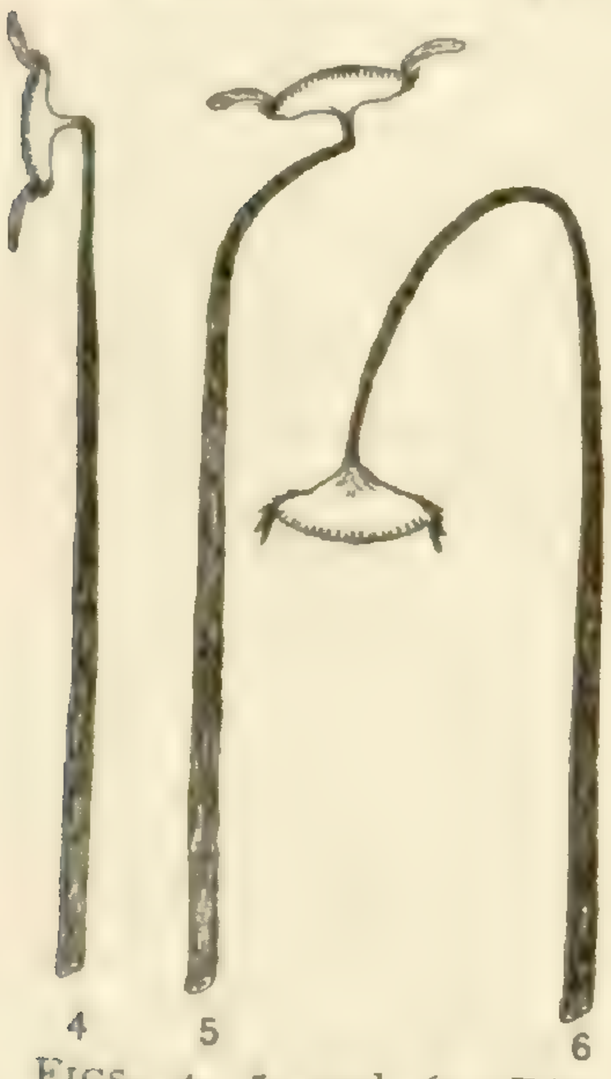


FIG. 3.—The same plant as in *fig. 2*, at 7 A.M. the next morning, showing eastward notation.

side of a house did not tip to the east but to the south. This may have been caused by the reflection of the sunlight from the wall. The eastward position is often disturbed by the wind, so that the heads may appear to face in any direction. Sometimes the heads tip to the east while the stem below still continues to nutate (*figs. 4, 5*). This condition gave a very unique appearance to the plant when nutating in the evening. The same phenomenon has since been observed also in wild *Helianthus annuus*. After the seeds begin to develop the weight of the head bends the stem over, and the sharp angle caused by the tipping disappears (*fig. 6*). *Fig. 1*, taken at six o'clock in the afternoon, shows well the mode of nutation and also the eastward tipping of some of the flowering heads. The tipping of the head is of advantage in bringing the bracts of the involucre



FIGS. 4, 5, and 6.—Diagrams showing tipping of heads at anthesis (4, 5), and position when fruiting (6).

into the best position for photosynthesis, and appears to be a definite physiological adaptation. The downward turning of the head which occurs later may be produced by the weight of the developing seeds, but it must not be forgotten that this is also a decided advantage. The whole large disk filled with seed is thus well protected from the rain, the dying bracts, no longer useful for food manufacture, forming a roof which sheds water very successfully. This position also permits

FIG. 7.—Wild *H. annuus*, 7 A.M. July 17, 1899, showing eastward nutation.

FIG. 8.—The same group of plants as in *fig.* 7, at 7 P.M. of the same day, showing the more prominent westward nutation.

the seed to fall readily to the ground and at the same time affords considerable protection from birds, many of which are very fond of the seed.

During the summer of 1899 some observations were again made upon the wild variety of *H. annuus*, in Clay county, Kansas. There is nothing new to add to the report in my former paper, but a number of photographs are presented showing the character of the nutation. *Fig.* 7 shows a group of plants at seven o'clock in the morning of July 17, and *fig.* 8 represents the same group at seven o'clock of the evening of the same day. The more pronounced nutation in the evening is very apparent. *Fig.* 9 shows a field of young sunflowers just at sunset on June 27. The plants in the foreground show the striking

effect of a large field of plants all bending to the west. The tipping of the heads to the east or northeast is at times very prominent. *Fig. 10* shows a small patch of plants with the heads in this position.

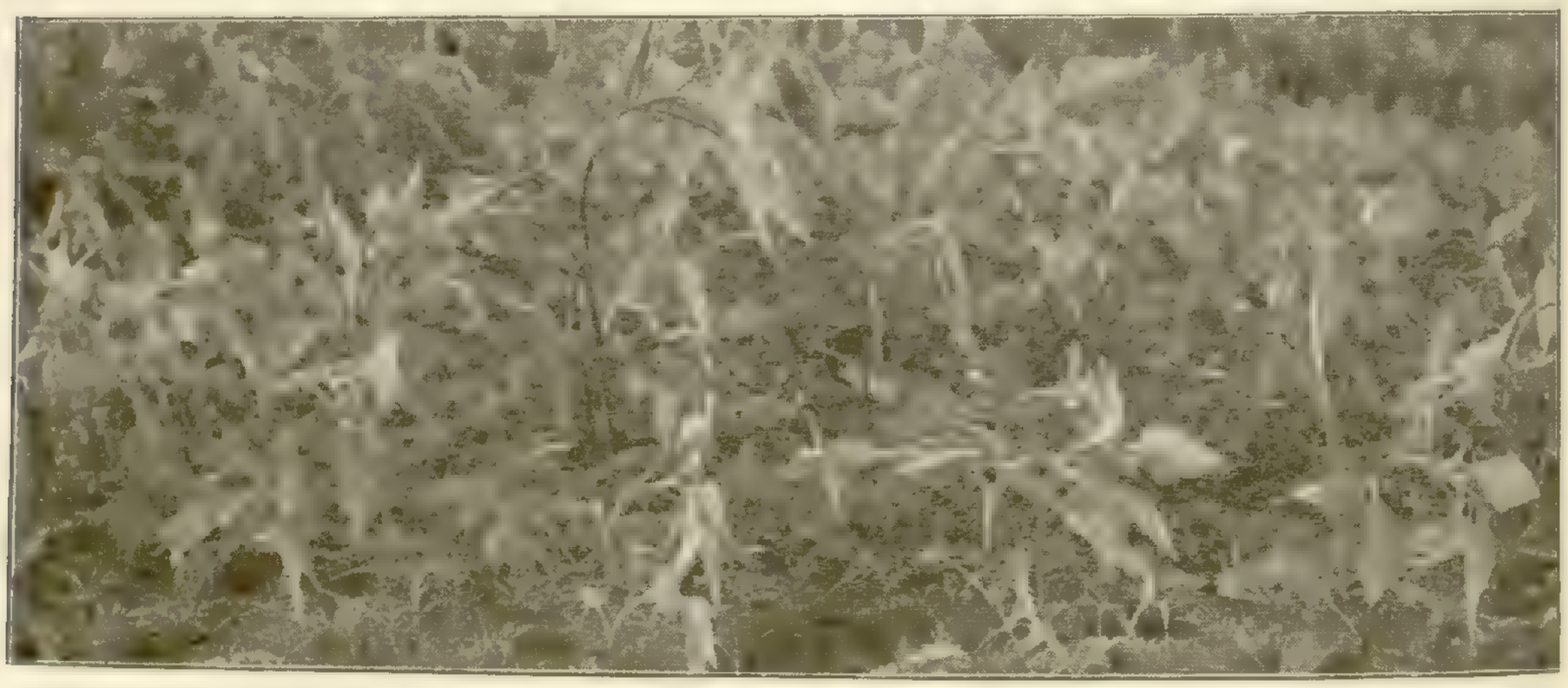


FIG. 9.—A field of wild *H. annuus*, just at sunset, June 27, showing the pronounced westward nutation in young plants.

The writer knows of no better plant for the study of the light relation of leaves than *Helianthus annuus*, and it can be made an object of great interest to the young student.

Some observations were also made upon *H. petiolaris*. It was observed to nutate 90° west in the evening, before the heads came into

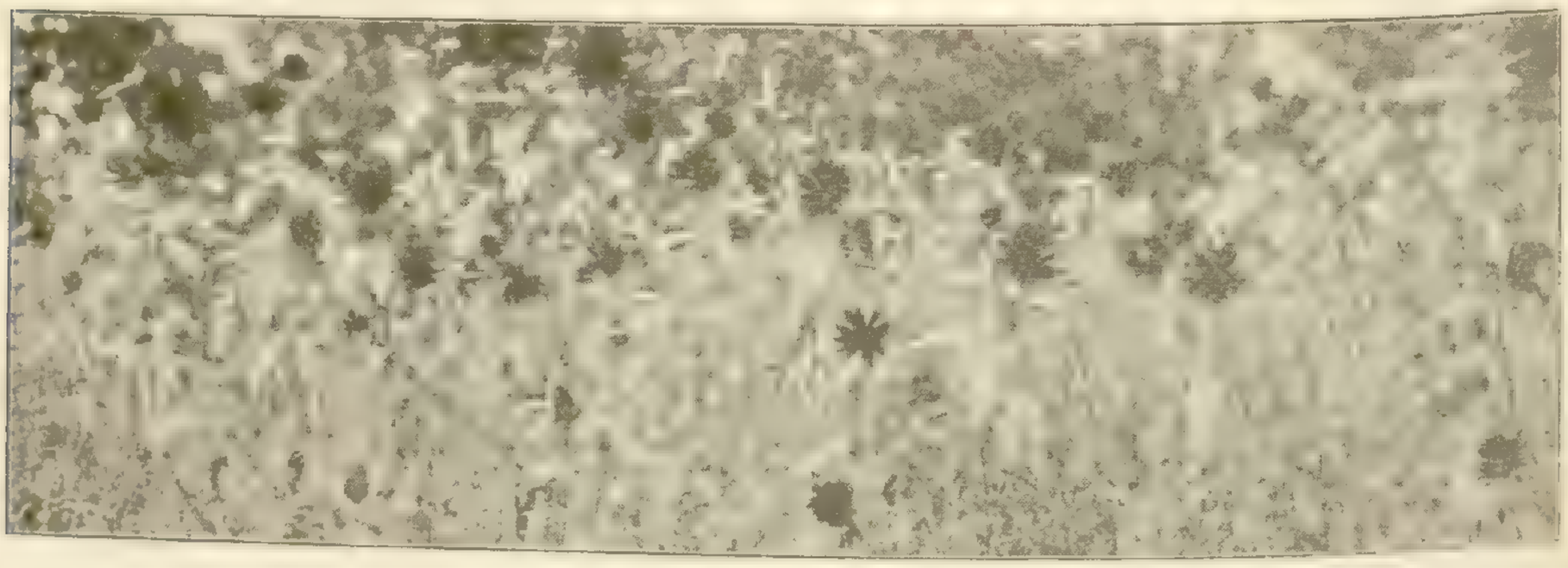


FIG. 10.—A patch of wild *H. annuus* at noon, August 23; the heads tip toward the northeast.

bloom, the nutation being nearly as marked as in *H. annuus*. On opening, the heads generally tip and the direction is usually to the northeast, at least for the terminal ones. But this movement is much less prominent than in *H. annuus*.—JOHN H. SCHAFFNER, *Columbus, Ohio*.

PTERIS CRETICA IN ILLINOIS.

THE CRETAN brake is a familiar plant in our dwelling houses and conservatories. It is said to be a native of Florida, Mexico, Guatemala, Italy, Corsica, Abyssinia, from the Ural mountains to Arabia, Himalayas, Philippines, Japan, and the Hawaiian islands.

In Mt. Carmel, Ill., it has long been one of the most common pot plants in our homes. About five years ago I first found it growing in my well, where it has continued to thrive ever since. Below about three feet from the surface it remains green throughout the year, and is now (February 15, 1900) thrifty and in all stages of development from mature fruiting specimens down to small plantlets.

Last summer I found it in a second well; and today it was shown me in a third. In each instance I learn that the plant has been cultivated in the adjoining house, whence the spores have probably found their way to the wells.

So I think it would be proper to add this beautiful fern to the introduced flora of Illinois, with this peculiar habit at the north.—J. SCHNECK, *Mt. Carmel, Ill.*

OPEN LETTERS.

THE RESEARCH STATION OF THE ROYAL BOTANIC GARDENS OF CEYLON.

I SHOULD like in a few words to call the attention of American botanists to the new research station which is now almost completed in these gardens, and to the advantages which are offered here to botanists desiring to work in the tropics. A more detailed account of the establishment under my charge, with plan of the new laboratory, will be found in *Nature* of November 9, 1899.

The Royal Botanic Gardens of Ceylon form a department of the public service, dating from 1812. In 1821 the headquarters were established at Peradeniya, a suburb of Kandy, from the center of which town the garden is about four miles distant. There are several good hotels in Kandy, and the gardens can be reached by rail or road ; a bicycle is perhaps the most convenient, and will be found very useful in traveling in the island, the roads being on the whole excellent. The garden lies in a very beautiful situation, in very mountainous country, at an elevation of 1550 feet above the sea. To this fortunate circumstance the garden owes the great advantage in the matter of climate and healthiness that it possesses over most other tropical stations. The nights here are always cool, and the neighborhood of Kandy is practically free of malarial fevers, so that with reasonable care no risk of health need be run in living here. The mean annual temperature is 76° F. The hottest months are March and April, with a mean temperature of 79°; the coolest January and June (74°). The laboratory and library are cool buildings, and in them during the last two years the extreme range of the thermometer has been between 65° and 82°. The annual rainfall is about ninety inches, fairly evenly distributed over the year; the wettest periods are in June and July and in November and December, at the beginnings of the southwest and northeast monsoons respectively. On the whole, the best time to visit Ceylon is from October to March ; but once here the climate is much the same all the year round, the objection to coming from Europe in the summer being the heat in the Red Sea and the discomfort of returning to a cold climate in winter.

The area of the garden is 150 acres ; it contains a splendid collection of tropical plants, and is arranged like an English park, with wide lawns. In the center lie the buildings of the museum, library, herbarium, and laboratory, close together. The museum is chiefly devoted to economic botany,

and contains a very good collection of local products. The library contains about two thousand books and papers, and is rapidly growing. About seventy periodicals are taken or received in exchange, and among them are included most of the important scientific botanical journals. The herbarium contains a Ceylon collection, a general tropical collection, and a collection of the plants growing in the gardens. The new laboratory for research lies to the north of the herbarium, and is a single-storied building 75 × 40 feet, including veranda on the west end. The length of the building runs east and west. On the north side are two rooms, one for general microscopic and morphological work, 36 × 18 feet, with four good working places, and one for physiological work, 18 × 18 feet, with two places. On the south side is a room for chemical work, 18 × 18 feet; a room for work in economic and pharmaceutical botany, 26 × 18 feet; and a small private laboratory, 18 × 10 feet. On the east end is a veranda, 8 feet wide, of which the two ends are built up so as to form a dark room and a lavatory, while the intermediate part forms a space 18 × 8 feet in which experimental work causing unpleasant smells or requiring open air can be carried on. The west veranda is partially closed in with a low trellis and wire netting to form a room for the breeding of insects, etc. The laboratory is fitted with the usual apparatus for work in botany, chemistry, and entomology. It contains altogether eleven good working places, of which five or six are usually occupied by the resident staff, leaving five or six available to workers from abroad, who will be heartily welcomed and given all reasonable facilities and assistance in prosecuting their researches.

The value to a botanist of a period spent in the tropics is inestimable, and there is no country more favorable than Ceylon for the study of every form of tropical vegetation within a limited area. Every variety of climate is found within the island, which has about six times the area of Jamaica, and can be easily reached by railway and coach, and there are good accommodations for travelers in almost every part of the colony. Branch gardens are kept up in four places in different climatic zones of the island. At Henaratgoda, on the main line of rail to Colombo, and eighteen miles from that town, there is a small garden of about forty acres, of which twelve are occupied by untouched jungle, the remainder being cultivated chiefly in economic plants; there is a small laboratory room in the garden and a resthouse about a mile away at the station. The climate here is very hot and steamy, the garden lying at thirty feet above the sea level. The rainfall is about 110 inches per year, distributed much as at Peradeniya, and the mean temperature is about 82° F.

A second branch garden is at Hakgala, at an elevation of 5600 feet. It occupies an extremely beautiful situation about six miles from the great sanitarium of Ceylon, Nuwara Eliya. The total area of the garden is 550 acres, of which 40 are cultivated, and contain a fine collection of European, American, Australian, and other temperate plants. The rest of the garden consists

of untouched jungle and savannah land, occupying the steep side of the Hakgala mountain to an elevation of 6800 feet. The vegetation of this high level region is very interesting; the flora contains a large proportion of European genera. The Horton Plains, where there is a resthouse at an elevation of 7200 feet, form a magnificent collecting ground for the botanist, and lie about eighteen miles from Hakgala. Nuwara Eliya, at an elevation of 6200 feet, contains good hotels, has a temperate climate (mean temperature 57°), and is surrounded by hills on which the natural vegetation remains untouched.

A third garden lies at Badulla, on the eastern side of the main mountain mass of the center of the island, at an elevation of 2200 feet. Here the climate is different from that at Peradeniya, in having the driest period at the end of the southwest instead of the northeast monsoon, so that the periodicity of the vegetation is different, and fruits which ripen at Peradeniya in April ripen at Badulla in August.

A fourth branch is at Anuradhapura, the famous "buried city" in the north of the island. Here there is an Indian climate and flora, the weather being dry during the greater part of the year, so that only xerophytic plants occur.

A visit to the branch gardens alone thus introduces the botanist to a great variety of climates and floras; but there are several other types of flora to be seen, *e. g.*, that of the coast, of the river estuaries, the mangroves, and so on: all are easily reached by rail or road. Ceylon is very easily reached, there being direct lines of steamers from Colombo to almost all parts of the world. Round the world tickets at a cost of $525 to $625, first class, can be obtained, which enable a visit to be paid to Europe, thence to Egypt and Ceylon, and home *via* Australia, or *via* Singapore, Hongkong, Japan, and Honolulu to San Francisco. Return tickets to Colombo from London are from $350 to $450 first class, $250 to $300 second class; the latter is very comfortable, especially on the French and German lines. No outfit is necessary beyond a supply of the clothes usually worn in summer; drill, khaki, and flannel clothes can be bought here more cheaply than in Europe. The cost of living in hotels and resthouses is from seven to nine rupees per day, and three rupees are equal to $1.

Information about Ceylon may be obtained in many books, of which the following may be specially mentioned: *Ceylon*, by Sir E. Tennant (now out of print); *Ceylon in 1893*, by J. Ferguson; "The flora of Ceylon as affected by climate," Trimen, *Journal of Botany*, 1886; *Flora of Ceylon*, Trimen, 1893–1899, 5 vols.; "Botanic gardens in the equatorial belt," Goodale, *American Journal of Science* 42: 173. 1891.

Intending visitors should communicate with me some time in advance, mentioning the line of work they propose to take up, with any special facilities they may require, *e. g.*, the planting before their arrival of special

experimental beds, the provision of any unusual apparatus or materials, and so on.—JOHN C. WILLIS, *Director Royal Botanic Gardens, Peradeniya, Ceylon.*

PATTERN FLOWERS AND METAMORPHOSIS.

C. R. B., in reviewing my text-book on p. 69 of the January GAZETTE, asks:

> Why assure a student that "a flower will obey certain well-defined laws," when the bulk of the chapters on the flower are concerned with explaining how they "disobey" these "laws," and in defining terms that are used to describe departures from a purely imaginative pattern? The whole treatment of the flower, indeed, proceeds upon the pernicious theory of metamorphosis.

Since the question has been asked, I trust that you will allow me to answer it, and in my own way.

My critic's quotation falsifies me, in sense as well as in word, and this falsification furnishes the only basis for his question. The statement is: "The typical flower will obey certain well-defined laws of structure as regards the following characters:" It may be wrong, but it at least allows its author the defense of reason, which is denied him by the misquotation. That statement was written in the light of an individual acquaintance with hundreds of such typical flowers, which the critic says are "purely imaginary." Since there are scores of thousands which vary from the pattern, the proportion of pages devoted to classifying such variations was considered appropriate. Is it not proceeding *ex cathedra* to call the theory of metamorphosis "pernicious"? May we not be credited with at least a knowledge of the attempts which have been made to get away from it, and a personal conclusion that that course leaves us no working basis which does not fail at the first test? To me the reading of Engler and Prantl's *Pflanzenfamilien*, and the actual study of the great number of flowers which I have examined during the last ten years is more convincing than any of the speculative "thought" or unproved theories which have been brought forward.—H. H. RUSBY.

[Dr. Rusby is quite justified in claiming misquotation, and I sincerely regret having been guilty of giving a false impression of his meaning, through my own misapprehension of the chapter criticized. My impression was derived from the chapter heading:

> LAWS OF FLORAL STRUCTURE AND THEIR (*sic*) DEVIATIONS,

and from the conspicuously printed "laws," thus:

> LAW 3: REGULARITY.— *The parts composing one circle are all of the same form and size.* A flower all of whose circles obey this law is regular. . . . .

Having examined these various laws and been impressed by their nullity, I was *not* impressed by the word *typical*, which occurs in two sentences of

the introductory paragraph only, though with general application throughout the chapter. I am blameworthy for this oversight; perhaps the author is not wholly blameless for the impression which led to it.

I also am stating a personal conclusion when I call the theory of metamorphosis pernicious. This conclusion is the basis of my criticism of the discussion of the flower. I call any theory or thinking pernicious which leads us to hold and to state a subjective conception as an objective reality. The fundamental postulate of the theory or metamorphosis is wholly conceptual in that it assumes a type or pattern for a member, such as a leaf, or group of members, such as a flower. The following, from p. 34, illustrates this and might have been written by Goethe himself]:

> Progressive metamorphosis also occurs. It is seen in the gradual transformation of bracts, themselves transformed leaves, into sepals in the barberry (fig. 61), and of sepals into petals and of petals into stamens (fig. 62) in the water lily. Even stamens may become metamorphosed into carpels and carpels into stamens, one instance being the flowers of the willow, where organs have been seen intermediate in appearance between the two.

How much better is that than Cesalpino's sixteenth century idea that the seeds are produced by the transformation of the pith? Would it not be better to state the facts, without alleging that a "transformation" occurs in the leaves, etc., which exists only in our imagination?—C. R. B.]

CURRENT LITERATURE.

BOOK REVIEWS.

The botanists of Philadelphia.

AFTER much correspondence and research Dr. Harshberger has published, as a contribution to the history of botany in the United States, a bulky volume[1] comprising the biographies of the botanists who have lived in or near Philadelphia. The limit has a 60-mile radius, which is comfortably large, as it takes in the cities of Lancaster, Bethlehem, Reading, and Easton, Pa., most of New Jersey except the extreme northern part, and a good part of Delaware. Within this liberal area, a considerable number of people are included, whose title to be ranked as botanists of Philadelphia is slight, either because of their transitory interest in the subject or the brevity of their residence in the city. Philadelphia has had enough real botanists of her very own to make an interesting book about, and we could have spared the incidental collectors (like Josiah Gregg), the distinguished physicians (like Dr. Horatio C. Wood), and pharmacists (like Dr. A. W. Miller), who may well be astonished at being called botanists.

But inclusiveness is easier than exclusiveness, and if one can find the facts he wants, he may pass by the ones he does not want. The inaccessibility of data about the dead, and the indifference or modesty of the living constitute only a few of the difficulties to be overcome in getting up such a book as this. The compiler, therefore, deserves cordial recognition for his thankless task, and leniency for the shortcomings which are doubtless more evident to him than to others.

After a general introduction regarding the topography of the region, a sketch of the botanical development of the city is given. This is followed by the biographical sketches, often accompanied by portraits and more or less complete bibliographies. Besides these a long list is given of persons whose biographies were not obtainable, lists of the members of the Philadelphia Botanical Club, of the Botanical Society of Pennsylvania, of the Philadelphia Moss Chapter, a historical account of the scientific journals and serial publications issued from Philadelphia (19 in number), a description of Horticultural Hall in Fairmount Park, and sketches of trees of historical or botanical interest.—C. R. B.

[1] HARSHBERGER, JOHN W.: The botanists of Philadelphia and their work. 8vo., pp. xii + 457, *pl. 48*. Philadelphia: The Author. 1899. $4.00.

The economic products of plants.

A VERY important addition to the literature on economic botany is a book by Dr. A. E. Vogl dealing with the nutritive and otherwise useful vegetable products and devoted largely to describing the microscopic structure and examination of these substances.[2]

The author fully recognizes the fact that a thorough knowledge of general morphology should precede any attempt to obtain definite information concerning this special field, and the book presupposes some such knowledge.

The cereal flours and their preparation are first discussed. The chemical and histological characters of the different kinds of flour are stated and these used as the basis of excellent tests of identity and quality. Reduction of the quality by poor preparation, adulteration, substitution, or by the presence of certain fungi receives due attention. That part of this chapter which deals with starch and the leading starch producing plants constitutes one of the most interesting features of the book. Starch from a large number of sources is figured and the differences shown in the size, form, and structure of the grains. Though the drawings of these starch grains are somewhat schematic, they serve the author's purpose quite well. At the close of the section is a key intended to assist in identification under the microscope of various kinds of starch.

The second division of the book deals with vegetables. The treatment is brief and closes with an especially interesting discussion of the edible fungi. Because of the usual environment of the mushrooms, and since they are frequently inhabited by insects and larvæ which may secrete poisonous substances, Dr. Vogl thinks the desirability of using mushrooms as food is open to quite serious question. A good key for distinguishing the usual edible fungi from the poisonous ones is given.

The subject of fruits is treated briefly while the chapter on *narkotische Genussmittel* deals largely with tea and coffee. Tobacco is omitted from this chapter. A very extensive and comprehensive chapter on spices is followed by the closing chapter on microscopical tests for the chief adulterants of pulverized spices.

Throughout the book the author deals with the economic product in question rather than with the detailed taxonomy of the plant yielding the product, a very wise departure from the plan too often used in works on this and similar subjects. Much attention is given to the morphology and histology of the various vegetable products. The chemistry of some of the products is discussed, but it is to be regretted that this feature is not more full. The drawings are copious, mostly well-made, and nearly all of them new, some being of structures not previously figured.

[2] VOGL, A. E.: Die wichtigsten vegetabilischen Nahrungs- und Genussmittel. Pp. xv + 575. *figs. 271.* Leipzig and Wien: Urban & Schwarzenberg. 1899.

A very prominent feature of the book is the description and illustration of substances used in substitutions and adulterations. These substances are treated in connection with the article adulterated or substituted, and the means of detecting them are made so clear that they will doubtless prove of great assistance. This is certainly one of the best works published upon the morphology and histology of the vegetable food products, their substitutes and adulterants. — OTIS W. CALDWELL.

Letters of two botanists.

THE LIFE-LONG correspondence between Unger and Endlicher, the two great Austrian botanists of that classical time of botanical reconstruction in the third and fourth decades of the century, has fortunately been preserved, having been bequeathed by Unger's heirs to the Botanical Institute at the University of Graz. Dr. Haberlandt has published these letters in chronological order, beginning with the date November 10, 1829, and ending March 16, 1847, two years before Endlicher's death.[3] The letters are preceded by a general résumé of the historical content and significance of the correspondence. Ample footnotes furnish the reader with bearings on contemporaneous botanical history. Indeed, in the opinion of the reviewer, these constitute the most instructive part of the book. Such a grouping of historical facts about the lives of these two men revivifies the history of those decades of reawakening in a way that plain historical accounts cannot approach. It is the application of the newer methods of history to botany, and will be welcomed as such by students of the history of botany. The work ends with a detailed account of Endlicher's death, including letters from his attending physicians which effectually refute the belief, current everywhere for a half century, that Endlicher took his own life. This idea was so firmly established that it found expression in nearly all biographical notices of the time, in lexicons, cyclopedias, and even in Sachs' *History of Botany*. These letters here published for the first time leave no doubt in the mind of the reader that the death of the patient was natural, the result of disease attended by a long period of suffering.

A perusal of the letters themselves, while not adding much that is new to the history of botany, gives us an astonishingly deep insight into the intellectual workshops and the personal character of the correspondents. The letters which preceded the *Genera Plantarum* will be enjoyed by all systematists. We are permitted to see for the first time the "Unger-Endlichersche System" in its original form, and to observe it from its inception through its various modifications to the time of its publication. It seems that more is

[3] HABERLANDT, G.: Briefwechsel zwischen Franz Unger und Stephan Endlicher. 8vo. pp. v + 184. Two portraits and facsimiles of two letters. Berlin: Gebrüder Borntraeger. 1899. *M* 5.

due to Unger than the *Genera Plantarum* would lead us to believe. Unger was anxious to furnish floral diagrams for the entire work, and offered four drawings to Endlicher as models. Although they were mutually agreed on the plan, it was for some unknown reason abandoned, and this phase of systematic botany was thereby retarded a score of years; for it was not until the days of Eichler that floral diagrams of comparable excellence with those originals of Unger first made their appearance.

We are reminded, too, in these days of ecological enthusiasm that there is nothing new under the sun; for even as early as 1836 Unger was actively engaged in the study of the influence of soil and climate on the distribution of plants, regarding a floral region as "ein meteorologisches und geognostisches Gemälde." To use his words: "A floral picture should be drawn, which must not only show its individual parts in the relations of space and time, but also the causal relations between external factors and inner life should be studied." Unger is therefore to be regarded as one of the founders of the biological or ecological method in systematic botany.—EDWIN B. ULINE, *Mankato, Minn.*

New elementary text-books.

THE past few years have witnessed many notable advances in education, but none more remarkable than the wonderful improvement in the teaching of elementary botany, at least in its theory. From its prevailing state of well-nigh barren formalism of less than ten years ago, it has leaped forward until it has become a vigorous and sympathetic representation of the science. This progress has been both marked and stimulated by a series of noteworthy works, the latest and most advanced of which is Professor Coulter's *Plant Structures*.[4] Not only does this work mark the highest degree yet reached in books devoted to the newer mode of teaching the science, but it probably marks the highest point it will reach, for it represents very nearly or quite the logical extreme of the tendencies of recent years.

Any consideration of such a work as *Plant Structures* must take account of it from two points of view: first, its botanical merit, and second, its adaptability to the purposes for which it was prepared. As to the former, the present reviewer has little but praise. That the work would be quite in touch with the present state of knowledge, both in fact and in spirit, was of course to be expected of its author, and this expectation is fully justified by the book. It is not entirely free from errors, but these are so slight as to be inappreciable in the general excellence of the work. It is written with great clearness, illustrated fully and beautifully, and as a whole proportioned judicially. Whether viewed from a botanical, a literary, or an artistic standpoint the book is admirable.

[4] COULTER, JOHN M.: Plant structures, a second book of botany. Pp. x+348. *figs. 289.* New York: D. Appleton & Co. 1899. $1.20.

Passing next to consider its adaptability to elementary teaching, it becomes at once evident that the author's aim has been not only to meet the best conditions of the present, but to lead the teaching of the science into a better estate. As a work intended for use either now or in the future, by beginners, however, it seems to the present reviewer not free from faults. Some of the subjects particularly emphasized, especially the alternation of generations and the morphological transitions from group to group, though immensely important and full of meaning to advanced students, are too abstract to be of either much interest or profit to beginners, whose basis of fact is extremely slender. The treatment of these topics is particularly lucid, but one cannot resist the impression at times that Professor Coulter, in writing these parts, had his colleagues rather than his students in mind. For this reason the book would seem better fitted for the use of students of some maturity, and especially for those who already have studied botany to some extent, and who wish to go over the subject systematically.

Again, the treatment of physiology seems not only inadequate in relative amount, but also unfortunate in mode. The former point may be met if the student uses the companion volume *Plant Relations*, which contains considerable physiology; but probably most students, especially most school pupils, will use only *Plant Structures*. Several of the leading physiological topics are not only at least as illuminating as some of the morphological ones, which the author treats so well, but they are equally capable of laboratory study and demonstration. Indeed taking the two volumes *Plant Relations* and *Plant Structures* together, they appear to the present reviewer weak in their physiological parts, notwithstanding the immense importance of physiology as a basis for ecology. Moreover, physiology, taken in one mass by itself, as in *Plant Structures*, is apt to prove rather indigestible, and experience shows that its topics may be more profitably considered along with the structures in which the work is principally carried on. The morphology of the flower appears also to have received hardly adequate treatment, especially in view of the fact that it is a subject generally misunderstood by our teachers.

But these latter criticisms have to do more with matters of opinion than of fact, and opinions may well differ. Upon one point however we can all agree; that Professor Coulter has given us a most excellent book, and one that is sure to prove both stimulating and serviceable.— W. F. GANONG.

IN EVANS'S *Botany for beginners*[5] we have a handy little volume with some good points, but on the whole very crude. The plan of combining laboratory directions with reading text is not unwise, but the author has attempted to cover too wide a field. He is coerced, perhaps, by the English *bête noir*, the examinations of the Science and Art Department, and although

[5] EVANS, ERNEST: Botany for beginners. 12mo. pp. viii + 290. *figs. 271*. London and New York: The Macmillan Company. 1899.

he disclaims an intention to make a "cram" book, it is essentially that. The condensation, the selection of unsuitable and sometimes impossible material and subjects for beginners, the numerous errors of fact, and the crudity of many of the illustrations, some of which are utterly misleading, render the book valueless to teachers in this country. That it receives the hearty approval of a well-known English botanist in *Nature* indicates the wide divergence of standpoint in the teaching of botany in the two countries.—C. R. B.

TO THE multiplying list of American schoolbooks Dr. D. T. MacDougal contributes a modest little volume,[6] the most elementary of the recent ones, outlining "a study of the functions or action of the plants," whose "organs are considered chiefly as instruments for the performance of work, with but little attention to their morphology." The author thus depends upon the pupil's previous knowledge of the parts of plants, a knowledge which is amazingly scanty and inaccurate. However, by careful selection of topics and simple presentation, the author ensures the pupil, in the main, clear notions of the work that plants do.

But some topics are introduced in whose presentation the author is sorely hampered and of which the pupil is quite certain to get wry notions, because there is too little basal knowledge of the structures concerned. The most notable instance is in the section on "the way in which new plants arise," wherein the alternation of generations is discussed; a topic which the very elementary character of the book might well be held to preclude.

Nearly all the few defects of the book are chargeable to the striving after vividness, simplicity, and brevity, which are so dangerous yet withal so necessary in a book of this grade. That Dr. MacDougal has succeeded admirably no one who has tried to write a small and simple book will deny. We commend it to teachers who wish to interest pupils in plants at work.—C. R. B.

MINOR NOTICES.

AN elaborate monograph on the hemp, *Cannabis sativa*, by Briosi and Tognini, has been completed by the issue of the second part,[7] treating in minute detail and most thoroughly the internal anatomy, the first part being devoted to the flowers. The whole monograph, comprising 271 quarto pages and 49 plates, is a monument to the late Dr. Filippo Tognini and to his botanical master and associate, Dr. G. Briosi.—C. R. B.

[6] MACDOUGAL, D. T.: The nature and work of plants: an introduction to the study of botany. 12mo. pp. xviii + 218. New York: The Macmillan Company. 1900. 80 cts.

[7] BRIOSI, GIOVANI E TOGNINI, FILIPPO: Intorno alla anatomia della canapa (*Cannabis sativa* L.). Parto seconda; Organi vegetativi. 4to. Dagli *Atti* dell' Istituto Botanico di Pavia II. 4: 168–315. *Pl. 4–29.*

THERE APPEARED, in 1896, as the Fourth Memoir of the American Folk-Lore Society, a volume by Mrs. Fanny D. Bergen entitled *Current Superstitions*, dealing "almost entirely with beliefs not of a zoological or botanical nature." Mrs. Bergen has recently contributed to the Memoirs of the same society another volume comprising, as its name *Animal and Plant Lore*[8] indicates, only the folk-lore of animals and plants. This book will be especially interesting to those who have followed in the GAZETTE the same author's lists of the popular names of plants.

The table of contents of the second part, on plant lore, is at the outset instructive and interesting. There is a chapter on amulets, charms and divinations, another on omens, a third on weather signs, a fourth on folk-medicine, and finally one devoted to miscellaneous items which is no whit behind the others in curious and, to the scientific mind, astounding data. This folk-lore is furnished from a great many states, east, west, north, and south, and, as Professor Bergen suggests in his very interesting introduction, "if we cannot detect in it morsels from every country in Europe, from half the tribes of Africa, from a large part of Asia and the great Pacific islands, as well as from many tribes of American Indians, it is only because our analysis is not sufficiently minute."

As to amulets we find that nutmegs are regarded as a true panacea, being used to prevent boils, croup, neuralgia, cold sores (this latter in the neighborhood of Boston!) earache and sties. Mountain ash is used as a charm both of a good and bad nature, while dandelions and southernwood are prominent in processes of divination. The chapter on folk-medicine adduces many folk-remedies, which although probably the result of pure empiricism are not without foundation in fact; *e. g.*, the wide use of various parts of the elder, *Sambucus* sp. Extensive notes supplement the data given in the body of the book.

The value of the work done by Mrs. Bergen in collecting this material now can hardly be overrated. It is to be hoped that it may be continued until the annals of our American superstitions are fully recorded.—RODNEY H. TRUE.

THE TWO LATEST REPORTS of the state botanist of New York, Mr. Charles H. Peck,[9] are for the years 1897 and 1898. They are in the main

[8] BERGEN: Animal and plant lore, collected from the oral tradition of English speaking folk; edited and annotated by Fanny D. Bergen with an introduction by Joseph G. Bergen. Memoirs of the American Folk-Lore Society, volume 7. 8vo. pp. x + 180. Published for the American Folk-Lore Society by Houghton, Mifflin & Co., Boston and New York. 1899.

[9] PECK, CHARLES H.: Report of the State Botanist for 1897. Reprinted from *Fifty first Ann. Rep. of the N. Y. State Museum:* 267–321, *col. pl. A–B, 50–56 in 4to.* Albany, 1898. 10 cents.

PECK, CHARLES H.: Report of the State Botanist for 1898. *Bull. N. Y. State Museum* no. 25, **5**:619–688, *col. pl. 57–61 in 4to.* Albany, Oct. 1899. 40 cents.

similar to those which have appeared annually since 1868. Two decades of continuous and uniform labor, of the excellent quality shown by New York's official botanist, is a record of which to be proud.

Both these reports, like two of the preceding, have the plates in quarto form, but they may be once folded and conveniently bound with the text in an octavo volume. An innovation is introduced with the last report by having it issued in the series of *Bulletins* of the Museum, instead of being part of the *Annual Report*, as heretofore.

Each report contains notes upon a large number of species of flowering and cryptogramic plants of the state of New York, in part recorded for the first time as occurring within its limits. In the 1897 report twenty-five species of fungi are described as new, and six species in the 1898 report. The detailed account of edible fungi, with colored illustrations, is continued, twenty-three species being added in these reports. In the last report there is also an account of the plants on the summit of Mt. Marcy, whose height is 5344 feet.— J. C. A.

THE VOLUME of biological lectures given at the Woods Hole Biological Laboratory in 1898[10] contains addresses of zoological interest chiefly. Some of the sixteen lectures treat large problems, and therefore deserve the attention of botanists, though the treatment is strictly from the zoological standpoint. The address by E. B. Wilson on the structure of protoplasm, that by S. Watasé on protoplasmic contractility and phosphorescence, and that by T. H. Montgomery on various nucleolar structures of the cell may be named as of most general interest. The volume should be indexed.

THE ELEVENTH annual report of the director of the Missouri Botanical Garden has been issued.[11] Extracts of the most general interest have already been given. The scientific papers include H. von Schrenk's paper on an important disease of cypress timber and a similar disease in the wood of the genetically related Libocedrus; J. N. Rose's description of the four agaves which flowered in Washington in 1898, including a new species, *A. expatriata;* J. B. S. Norton's monograph of the North American euphorbias of the Tithymalus group, amounting to nearly forty species, and several new varieties, all of them figured on good plates; and J. G. Smith's revision of the half dozen United States Species of Lophotocarpus, together with a description of a new species of Sagittaria, *S. Eatoni.* The volume needs an index.

NOTES FOR STUDENTS.

EXPERIMENT STATION BULLETINS dealing with plant diseases, not heretofore mentioned in these pages, are as follows: A. P. Anderson (S. C. no. 41: 3–14. *4 figs.*) describes "Rice blast and a new smut on the rice plant,"

[10] 8vo. pp. iv + 343, illust. Boston: Ginn & Co. 1899.

[11] 8vo. pp. 151, *pl. 58.*

the cause or causes of the first trouble being conjectured, and that of the second being identified as *Tilletia corona* Scrib.; while Ernest Walker in the same bulletin (p. 15–31, *1 fig.*) discusses "Treatment for rice smut," showing by tests that a number of fungicidal methods are available, but owing to failure in germinating the smut spores their efficiency was not determined. A. B. Cordley (Ore. no. 57 : 3–15. *1 pl. 7 figs.*) gives an account, under the title "Brown rot," of the injury to fruit in Oregon, due to *Monilia fructigena* Pers., together with a study of the fungus. H. H. Lamson (N. H. no. 65 : 99–108. *6 figs.*) gives "Notes on apple and potato diseases in 1898," with tests of fungicides. A. D. Selby (Ohio no. 97 : 31–61. *4 figs.*) presents considerable data upon smut, rust and scab of wheat and smut of oats. The Fusarium causing wheat scab has been traced to an ascigerous condition, believed to be identical with *Gibberella Saubinettii* Sacc. Results of treatment of seed grain to prevent the several smuts, J. F. Hickman being associated with this part of the work, are tabulated. A. D. Selby (Ohio no. 104 : 201–216. *3. pl.*) also shows the beneficial results obtained by spraying for peach curl, and gives a few notes on crown gall and yellows of peach. The same investigator (Ohio no. 105 : 217–235. *2 figs.*) publishes "Further studies of cucumber, melon and tomato diseases," with some account of the fungous and bacterial causes, and the results of spraying. F. A. Sirrine and F. C. Stewart (N. Y. no. 156 : 375–396. *4 pl.*) cover part of the same ground with statistics on "Spraying cucumbers in the season of 1898." A popular description of "The black rust or summer rust" of grains is given by Otto Lugger (Minn. no. 64 : 535–550. *13 figs.*) Methods for "The prevention of the smuts of cereal grains, and prevention of potato scab" are presented by H. L. Bolley (N. D. no. 37 : 363–379. *3 figs.*) with some results attained by farmers. H. Garman (Ky. no. 81 : 3–11. *2 pl. 1 fig.*) tells of "A method of avoiding lettuce rot" under glass by employing a system of sub-watering, and also gives the results of "Potato scab experiments made in 1898" in the use of fungicides. A. P. Anderson (S. C. no. 38 : 3–15. *5 figs.*) writes on "The asparagus rust in South Carolina," and G. E. Stone and R. E. Smith (Hatch, Mass. no. 61 : 3–20. *2 pl.*) write on "The asparagus rust in Massachusetts." J. C. Blair (Ill. no. 54 : 181–204. *27 figs.*) gives directions for "Spraying apple trees with special reference to apple scab fungus;" S. T. Maynard (Hatch, Mass. no. 60 : 3–11) provides formulæ for "Insecticides, fungicides," accompanied by a "Spraying calendar;" while W. M. Munson (Me. no. 52 . 3–8) gives general directions and formulæ for "The spraying of plants." A. L. Quaintance (Fla. no. 46 : 77–114. *12 figs.*) provides a rather full account of the strawberry thrips (*Thrips Tritici* Osb.) and of the onion thrips (*Thrips Tabaci* Lind,). and of the nature of the injuries they cause to plants. G. E. Stone and R. E. Smith (Hatch, Mass. no. 55 : 3–67. *12 pl.*) give a large amount of information about "Nematode worms" (*Hederodera radicola* Müll.), including historical and experimental data, much of it new, and with

illustrations showing the development of the worms and the production of galls on the plants. C. P. Close (N. Y. no. 161 : 153–164. *2 pl.*) records three season's tests in successfully combating gooseberry mildew with potassium sulfid, and less important results with Bordeaux mixture, lysol, and formalin. A popular two-page edition of this bulletin has been prepared by F. H. Hall.— J. C. A.

ANNUAL REPORTS of experiment stations published during the year 1899 not yet mentioned in these pages but containing matters of interest to botanists, may now be briefly noticed. In the nineteenth report of the New Jersey station B. D. Halsted (pp. 289–370, *12 pl.*) fills eighty pages with the results of a wealth of observation and experiment, supplemented with a dozen well printed plates. Lime is found to be effective in checking club-root (Plasmodiophora) of turnips, and sulfur ineffective; the latter, however, when applied to the soil outranked corrosive sublimate in reducing the scab of potatoes, and it is even more serviceable in case of sweet potatoes. The fungicides, Bordeaux mixture, cupram, soda-Bordeaux, and creolin, were used with varying results upon beans for *Colletotrichum lagenarium* Pass. and *Bacillus Phaseoli* Sm., on tomatoes for *Cladosporium fulvum* Cke., on spinach for a Cladosporium and a Phyllosticta, on egg-plants for *Phyllosticta hortorum* Speg., on cucumbers for *Colletotrichum lagenarium* Pass., and on beets for *Cercospora beticola* Sacc. Fungicides were also used on other plants with less conspicuous results. The smut of onions, *Urocystis Cepulæ* Fr., was introduced into a plat by bringing soil from another part of the state which had borne a smutted crop the year previous. There are observations upon asparagus rust, and on other parasitic fungi, on shading plants, on weeds, and on a number of other topics. The report closes with a discussion of the relation of fungi to weather.

In the eleventh report of the Hatch experiment station of Massachusetts, George E. Stone and R. E. Smith (pp. 142–167) record observations upon the occurrence and injury of Alternaria on muskmelon, rust on chrysanthemum, *Colletotrichum Violæ-tricoloris* on pansies, and of other parasitic fungi. Rather more space is given to physiological disorders of lilies, roses, cucumbers, and shade trees, being chiefly due to over feeding and to gas poisoning.

In the twenty-second report of the Connecticut station W. C. Sturgis (pp. 225–267) discusses the appearance and prevention of three melon diseases: wilt caused by *Bacillus tracheiphilus*, blight caused by *Alternaria Brassicæ*, and burn due to a sudden disturbance of equilibrium between water absorption and evaporation; of the mildew of lima beans and of the calico and spot diseases of tobacco. There are also seven pages of miscellaneous notes on plant diseases and spraying. In the same report E. H. Jenkins (pp. 310–316) gives statistics on the germination of garden seeds of various ages.

In the fourteenth report of the Maine station L. H. Merrill (pp. 64–74, *7 pl.*) reports in an interesting way upon box experiments with phosphoric acid from different sources. In the same report F. L. Harvey (pp. 131–135) has brief notes on weeds. Also W. M. Munson describes "The blueberry in Maine" (pp. 164–172, *2 pl.*), including four species, *Vaccinium Pennsylvanicum* Lam., *V. vacillans* Sol., *V. nigrum* Britt., and *V. Canadense* Rich., with notes on their culture; he reports experiments on "The acquisition of atmospheric nitrogen and soil inoculation" (pp. 208–212), and he has also a carefully prepared article on the behavior of pollen during fertilization and its after effects in formation of the fruit (pp. 219–229, *5 pl.*), which was in part presented before the Society for the Promotion of Agricultural Science at the Boston meeting in 1898. In the same report W. M. Munson and L. J. Shepard record experiments showing great superiority of crop from large seeds over small seeds of radish (pp. 158–160), and the conspicuous advantages of sub-watering over surface watering in growing radishes under glass (pp. 161–163. *1 pl.*).

In the eleventh report of the Rhode Island station Fred. W. Card (pp. 106–110, *7 pl.*) records the first season's results with apple trees having roots and branches pruned in various ways at time of planting. In the same report H. J. Wheeler and J. A. Tillinghast (pp. 122–191, *19 pl.*) give an interesting and instructive account of varied plat experiments in feeding plants and the use of "nitragin." In the same report J. A. Tillinghast (pp. 192–203) shows by statistics the effectiveness of the hot-water treatment of oats for smut, and the less value of the commercial "ceres pulver."—**J. C. A.**

BULLETINS from the experiment stations on medicinal and poisonous plants are as follows: C. W. Hyams (N. C. no. 150: 329–409) gives a list of over 800 species of wild plants of North Carolina having reputed medicinal virtues. They are arranged systematically under the Latin names, their poisonous or useful properties noted, and an index appended. It is a useful publication. B. D. Halsted (N. J. no. 135: 3–28, *4 pl. 2 figs.*) gives an account of the plants of New Jersey which are poisonous and liable to be eaten by men or animals, or are poisonous to the touch. It embraces much detailed and useful information. F. W. Morse and C. D. Howard (N. H. no. 56: 111–123, *6 figs.*) have investigated the "Poisonous properties of wild cherry leaves," testing the black cherry (*Prunus serotina*), choke cherry (*P. Virginiana*), and the red cherry (*P. Pennsylvanica*). All were found to be decidedly poisonous, the black cherry especially so. The youngest and most succulent leaves contain the most poison, which is increased somewhat by wilting, and partially lost by drying. The bulletin is an important contribution to our knowledge of the wild cherries. E. V. Wilcox (Mont. no. 15: 37–51, *3 pl.*) reports upon the poisoning of sheep by eating larkspur (*Delphinium Menziesii*), both unintentionally while grazing and experimentally by use of a fluid extract.—**J. C. A.**

MISS MARIA DAWSON has studied the tubercle organism and the mode of infection in *Vicia hirsuta* and *Pisum sativum*.[12] Her results confirm those of previous observers as to the mode of infection by tubes traversing one or more root hairs into the cortex. These tubes have the advancing end open and consist of numbers of straight rodlets with longer axes arallel to the line of growth of the tube. Finally, after traversing a cell, the tube bursts on one side and sets free the rodlets in the cell cavity. (No such infection tubes were found in Lupinus and Phaseolus.) The matrix enclosing the rodlets contains nothing of the nature of cellulose or chitin, or (probably) mucilage. These characters are conclusive against the organism being one of the true fungi, and call to mind Prazmowski's view that it is a filamentous zoogloea form of a schizomycete, and also Thaxter's Myxobacteriaceæ. Drop-culture experiments, the first of the kind, enabled the author to follow the multiplication of the rodlets by constriction and separation, the process being completed in 2–4 hours. Bacteroids were also developed in these cultures, but the author has not yet been able to observe the process of their development. Experiments were also made with "nitragin," which showed that it contained the tubercle organism and induced tubercle formation by direct application to seeds or through the soil.—C. R. B.

IN THE *Journal* of the Cincinnati Society of Natural History (19: 147–166. 4 Jan. 1900) Dr. A. P. Morgan publishes his fifth paper on the Myxomycetes of the Miami valley, Ohio, in which he presents various systems of classification of this group, some of them of only historical interest. The paper closes with his own grouping of the genera of North America, under four sections, with analytic keys to the genera.—C. R. B.

NO DOUBT students of histology will be interested in hearing how, according to the editor of *Meehan's Monthly*, trees increase in diameter. Explaining how a label was overgrown instead of being pushed outward he writes: "To those who understand the manner in which new wood forms, the explanation is simple. The increase in the girth of trees takes place during a few weeks at midsummer, and is by the rapid multiplication of minute cells. These, at first, are as soft as mush, and might be compared to the flow of so much yeast. If the flow is checked in one direction, it turns to the direction its neighbor is journeying, and adds itself to the volume of that stream." The persistence of erroneous ideas is amazing.—C. R. B.

STUDENTS of grasses will hardly look for articles on that group in the *Revue Bryologique*. Yet the opening number for 1900 contains two by N. Orzeszko of Nice; one on the processes for securing good sections of dried leaves of grasses, *i. e.*, for histological study of herbarium material, and a second consisting of an elaborate code of signs for histological description of

[12] Phil. Trans. Roy. Soc. London B. 192: 1–28. 1899.

grass leaves. The former may be of some service; such schemes as the latter embodies are useful enough for the note book, but only cumber literature.—C. R. B.

OUR KNOWLEDGE of the life history of the Gnetaceæ has been considerably increased by Lotsy's[13] recent work on the life history of Gnetum. The difficulty in procuring material is responsible for the fact that comparatively few observations have been made. Of the three genera which compose the group, Welwitschia is found only in Damaraland, Ephedra is a desert plant, and the remaining genus, Gnetum, is found only in the tropics. Moreover, as in case of most gymnosperms, the collecting must extend over a considerable period in order to insure anything like a complete series of stages.

Dr. Lotsy's stay at the Buitenzorg botanical gardens in Java enabled him to secure a very complete series of stages in the development of *Gnetum gnemon*, from the earliest appearance of the flowers up to the formation of the embryo.

The inflorescences of *Gnetum gnemon* are spikes which come from the axils of opposite bracts. On each spike is a series of cups which owe their origin to a concrescence of bracts. At the base of each cup is a ring of tissue, upon the upper part of which may be seen a number of small, cone-shaped, greenish bodies; these are the female flowers. The mature female flower has three envelopes, which are formed in acropetal succession. The rudimentary female flowers found on the staminate spikes have only two envelopes.

The author regards the outer envelopes as whorls of bracts, which, for convenience, may be called the internal and external perianths. The inner envelope, which is longer and projects above the other two, he regards as an integument.

At the period of pollination a drop of fluid appears at the top of the integument, and consequently the term integumental stigma is applied. Pollination is probably effected by the wind, though it may be that insects have some part in it.

There is a pollen chamber at the top of the nucellus, formed by the degeneration of cells in that region. Before reaching the embryo-sac the pollen tube contains a tube nucleus and two generative nuclei. The details of spermatogenesis are reserved for a future paper. Each nucellus contains several macrospores which originate as in well-known gymnosperms. The early divisions in the macrospore do not seem to differ from those in Pinus or other familiar forms, there being first a series of nuclear divisions, so that a large number of nuclei lie free in the protoplasmic lining of the embryo-sac. The history from this stage differs from that of other gymnosperms. A constriction appears somewhat below the middle of the sac, reducing the lumen

[13] LOTSY, J.: Contributions to the life history of the genus Gnetum. Ann. du Jardin Bot. de Buitenzorg. II. 1: 46–114. *pl. 2–11*. 1899.

at this point, but by no means separating the upper and lower portions. Walls now appear in the lower portion so that it becomes filled with solid tissue at the apex of which bodies which may be rudimentary archegonia are sometimes found. In the upper portion the nuclei remain free in the protoplasmic lining of the sac.

At this stage, one or more pollen tubes enter, each bringing in two generative nuclei. Each generative nucleus fuses with one of the free nuclei in the sac, and the several copulation products become surrounded by denser protoplasm and soon acquire a membrane. They are now called zygotes. The zygotes germinate into long tubes, which grow down toward the base of the sac and penetrate the solid tissue there. Previous to this time this prothallial tissue has been increasing enormously and in the mature seed the fertile portion of the sac appears as a mere speck at the apex of it. At this stage the seed falls from the plant.

The development of the embryo from the tube which arises from the zygote has already been described by Bower.

The author suggests the following homology with the structures of the angiosperm sac.

Angiosperms		Morphological nature		Gnetum gnemon.
Egg apparatus	=	Archegonia	=	Fertile nuclei.
Micropylar polar nucleus	=	Prothallium	=	Sterile nuclei of upper part of sac.
Chalazal polar nucleus	=	Prothallium	=	Prothallium in lower part of sac.
Antipodals	=	Rudimentary archegonia	=	Rudimentary archegonia on lower part of sac.
Endosperm	=	Prothallium	=	Growing prothallium of lower part of sac.

The conclusion is reached that the Gnetaceæ are very ancient in origin and that they must have originated before or at the same time with gymnosperms (by this probably meaning the Coniferæ.)

He is inclined to regard "the Gnetaceæ as the equivalent of the gymnosperms and angiosperms combined and running parallel to these, having originated entirely independently of them. In these two parallel rows the gymnosperms may be compared to the Ephedroideæ and the angiosperms to the Gnetoideæ."

There will be objections to this interpretation if current views as to the geological history of the group are well founded.—CHARLES J. CHAMBERLAIN.

DATA bearing on the problem of the sexuality of the lichens are gradually accumulating, and the most recent contribution is by Darbishire[14] on *Physcia*

[14] DARBISHIRE: Ueber die Apothecienent wickelung der Flechte *Physcia pulverulenta* (Schreb.) Nyl. Jahrb. f. wiss. bot. 34: 329. 1899.

pulverulenta. His investigations extend and support the results of Baur (1898). It will be remembered that Baur found again the trichogynes discovered by Stahl in members of the Collemaceæ, observed the sperms fused with their tips, and saw stages indicating that the trichogyne withered from above downward after fertilization.

Darbishire finds the archicarps each with its trichogyne in the youngest portions of the lichen thallus, and so very numerous that 700–1200 may be present on a small lobe. The lower part of the archicarp is an hypha of two or three loose coils, and is situated below the layer of algal cells about midway between the upper and lower surface of the thallus. The multicellular trichogyne extends as a filament between the algal elements to the exterior, where it projects above the upper surface. Sperms were observed attached to the tips of the trichogynes, but older stages show only one fused with each structure. When an archicarp of the group is fertilized it immediately develops rapidly, and, although others may show signs of fertilization and apparently start to develop, they finally disappear, and only one apothecium is formed.

After fertilization some of the large cells in the middle region of the coiled archicarp enlarge and finally fuse, so that there results a swollen multinucleate cell, the ascogonium, in each lobe of which lies a nucleus. A system of much branched hyphæ arises from the ascogonium, becoming the ascogenic hyphæ, from which the asci arise. The paraphyses develop from sterile hyphæ around, but entirely distinct from the ascogenic ones; the two systems of hyphæ being readily distinguishable. The further development of the apothecium follows closely the older accounts.

This investigation supports at all essential points the studies of Baur, and extends the evidence of sexuality to another family of lichens. It suggests the probability of the presence of trichogynes and the sexual act in many more groups than most botanists have been willing to admit in the past. In passing we should also note that the recent suggestion of Lindau in respect to the function of trichogynes appears very dubious. He has presented (1899) a theory that the trichogynes are organs whose function is to bore through the layer of algal elements to the surface of the lichen, thereby weakening this layer and allowing the apothecium to develop more readily and to push up from below. Darbishire shows that such a function for the trichogynes of *Physcia pulverulenta* is quite impossible, and that this operation is performed by the developing paraphyses.

We should bear in mind that whatever are the probabilities of sexuality among the lichens, we have not the knowledge that may be regarded as proof positive. We do not know the fate of the nucleus from the sperm, whether or where the fusion of sexual nuclei takes place, and withal we have a complexity of conditions in the multicellular trichogyne that is certainly very puzzling.—B. M. Davis.

A VERY clear paper by Dr. A. Nabokich, on the functions of aerial roots of orchids has appeared in *Botanisches Centralblatt* 80: 331 *et seq.*, 1899. He shows that the supposed power of their velamen to condense water vapor from the atmosphere does not exist, and presents good evidence that these roots can make use of dew only as it condenses on leaves and stems and reaches them in drops. He proves that though they supply the plant with water, there is no correlation between transpiration and absorption, where there is storage of water. Absorption decreases with the temperature of the water, and when the storage factor was eliminated by the saturation of the tissue, there was little or no absorption in cold water if transpiration was prevented. He recognizes no relation between the presence of leaves with water storage and the presence or absence of velamen. The chief function of the velamen, he considers to be the protection of the parenchyma from sudden cooling at night, especially in the dry season, and in support of this view he lists nearly three hundred species showing the relation between the presence of velamen and the environment of the species. Those in moist, equable regions show at most only a few layers of the velamen, while those living under more variable conditions have from a few to eighteen layers. A second function of the velamen is the power of adapting the roots to hydrophytic conditions during the rainy season, when they are encased in water, and he believes the "white streaks" to be air reservoirs to allow them to breathe at this time.—L. M. SNOW.

UNDER THE title "The sexuality of the fungi," Harold Wager presents[15] a summary of the present knowledge regarding nuclear fusions in the fungi, and considers the leading interpretations which have been given to the facts. Wager regards it as possible that in Sphærotheca and similar forms the development of the ascogonial filament of cells exhausts the energy imparted by the preceding fusion of the antheridial and oogonial nuclei; that the energy necessary to produce another reproductive cell, the ascus, can only be obtained by a further nuclear fusion; and that in the higher Ascomycetes this second nuclear fusion has probably replaced altogether the morphologically sexual fusion of the simpler forms. This hypothesis may be extended to embrace the Ustilaginales and Uredinales.

It may well be that a deeper insight into sexuality itself and a due consideration of the later developments in physiology[16] will lead to views involving less of the idea of an energized nucleus.—F. L. STEVENS.

[15] Annals of Botany 13: 575–597. 1899.

[16] LOEB, JACQUES: Am. Jour. of Phys. 3: 135–138. 1899.

NEWS.

MR. WALTER R. SHAW has been appointed assistant professor of botany at Pomona College, Claremont, Col.

MR. A. I. ERIKSSON (Tufts College) has issued a catalogue of natural history books and authors' separates which will be of interest to botanists.

THE ANNUAL meeting of the American Association for the Advancement of Science will be held at Columbia University, New York, June 25–30, 1900. Titles and abstracts of botanical papers should be sent at once to the secretary of Section G, Dr. D. T. MacDougal, N. Y. Botanical Garden, N. Y. City.

ACCORDING TO the *Revue Bryologique* Dr. A. J. Grout, of the Boys High School, Brooklyn, N. Y., is intending to publish *exsiccati* of the pleurocarpous mosses of North America, "with the cooperation of the principal American bryologists." The first set, of twelve numbers, has just appeared. The price is to be $7.50 per century.

THE LAWRENCE SCIENTIFIC SCHOOL of Harvard University has issued a preliminary announcement of a four-year course in landscape architecture, including botany in the first year, horticulture in the second, a study of plants in relation to landscape planting in the third and fourth years, and the infirmities of plants in the fourth year.

THE FIFTH annual mid-winter meeting of the Vermont Botanical Club was held at the University of Vermont, January 26 and 27. Many papers of general as well as of local interest were presented and discussed. The following officers were elected: president, Ezra Brainerd; vice president, C. G. Pringle; secretary and treasurer, L. R. Jones.

PROFESSOR RYŌKICHI YATABE, founder of the Botanical Society of Japan, and for ten years its president, was drowned September 10, 1899, at Kamakura, where he was spending the summer. He studied in America and was the first professor of botany in the Imperial University of Japan. The December number of the Tokyo *Botanical Magazine* contains a fine portrait of him.

DR. N. L. BRITTON asks the BOTANICAL GAZETTE to announce that pressure of work during the latter part of last year made it impossible at that time for him to bring his address as retiring president of the Botanical Society of America into satisfactory form for the usual publication. The

substance of the address, however, will appear in *Bulletin no. 5* of the New York Botanical Garden, now in press.

WITH THE conclusion of the seventh volume, December 1899, M. Eugène Autran announced that the publication of the *Bulletin de l'Herbier Boissier* terminates. It will be welcome news to taxonomists, who have learned to look to the *Bulletin* for work of the highest quality, that a successor has already appeared in the *Mémoirs*, having much the same form, but consisting of a series of separate papers issued at irregular intervals.

PRESIDENT HADLEY has made the welcome announcement that a school of forestry is to be established at Yale University. It is promised that the "principles of botany" are to form an important part of the instruction. It would be most gratifying to botanists if the science in its modern aspects and development should be fully presented at Yale, which, in this particular, has long lagged far behind most western institutions and her great New England rival, Harvard.

THE FIRST number of the *Journal* of the New York Botanical Garden was issued with the beginning of the year. It is an interesting 16-page number, with a late photograph of the museum building as a frontispiece. The *Journal* is to be edited by Dr. D. T. MacDougal, and will be published monthly, containing illustrated non-technical articles, news, notes, etc., of general interest. The publications of the Garden now comprise four series: the *Journal*, the *Bulletin*, the *Memoirs*, and the *Contributions*, the latter including reprints from publications other than the first three. Such multiplication of titles is unfortunate, because it increases the chances for error in citation and the labor of keeping track of publications. The Garden is following the bad example of some older institutions in this respect, notably the Buitenzorg Garden, which has recently established the *sixth* series of its publications. We wish the New York Garden would lead a reform in this respect.

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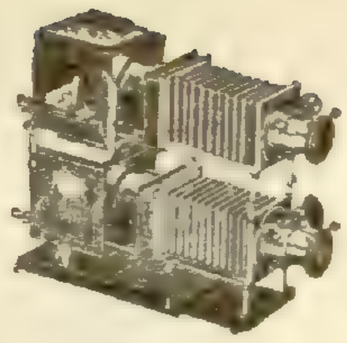

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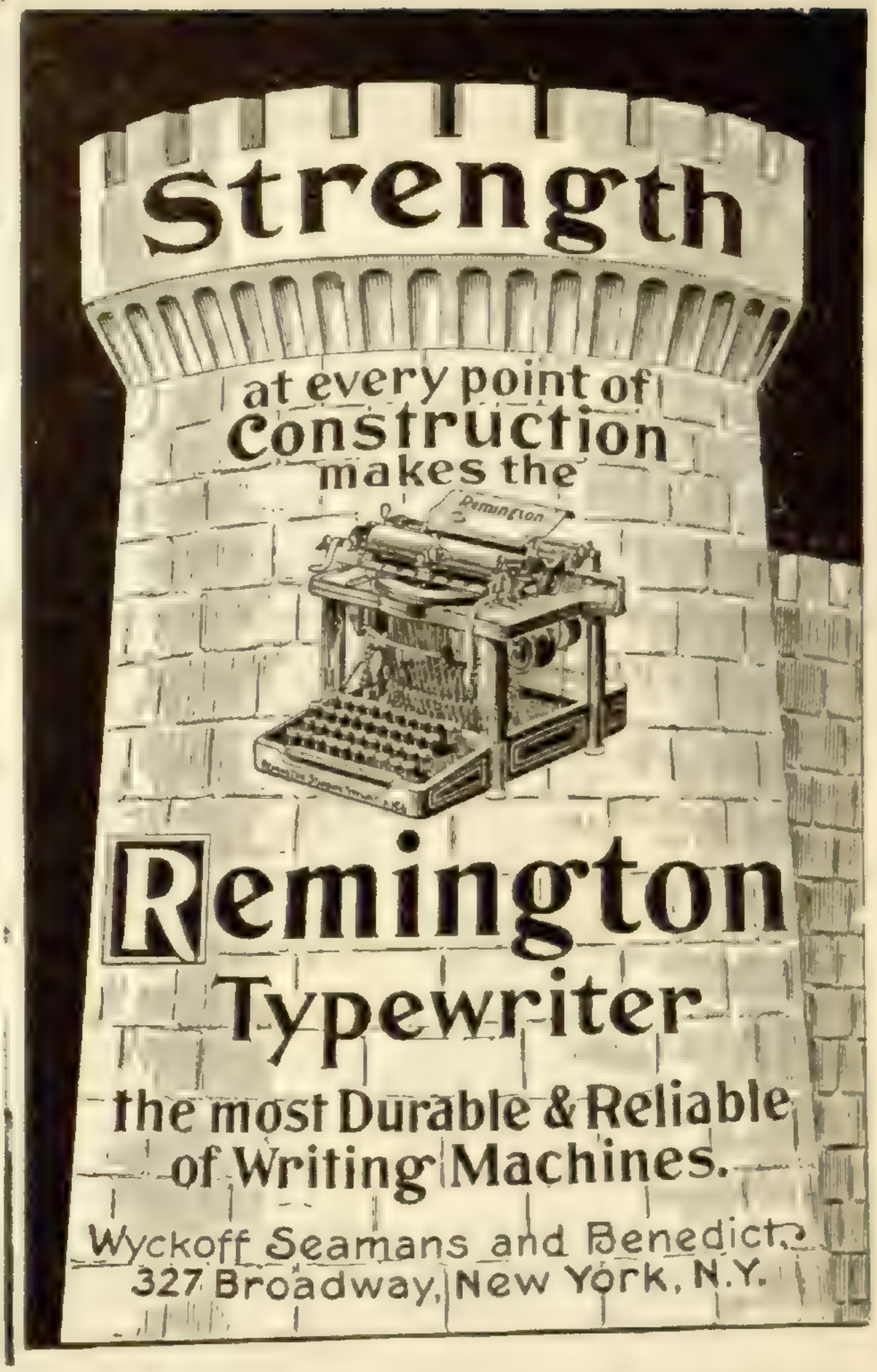

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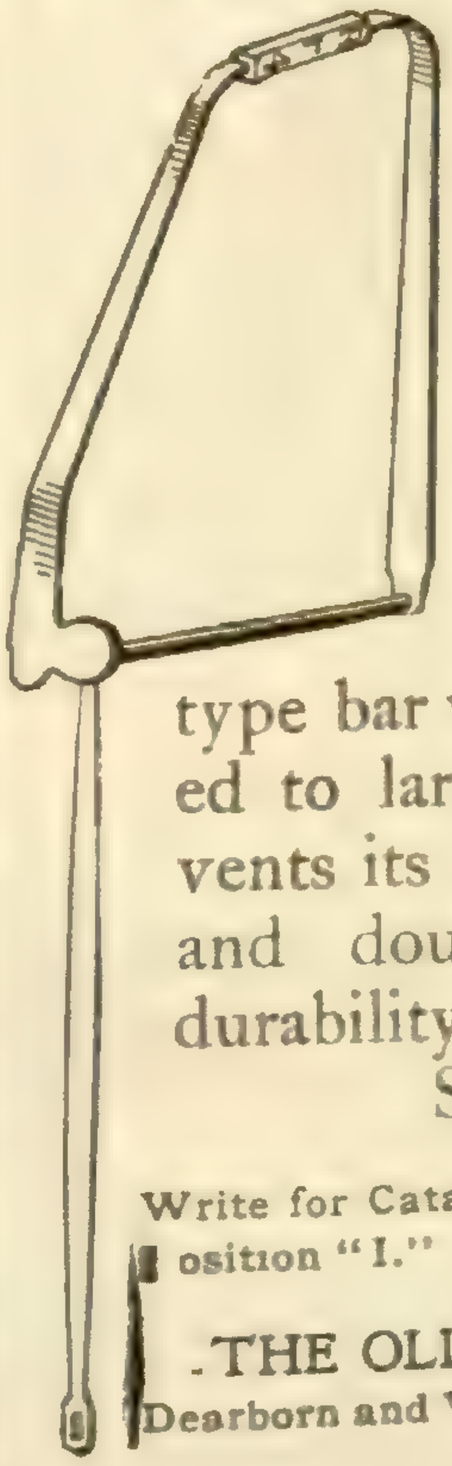

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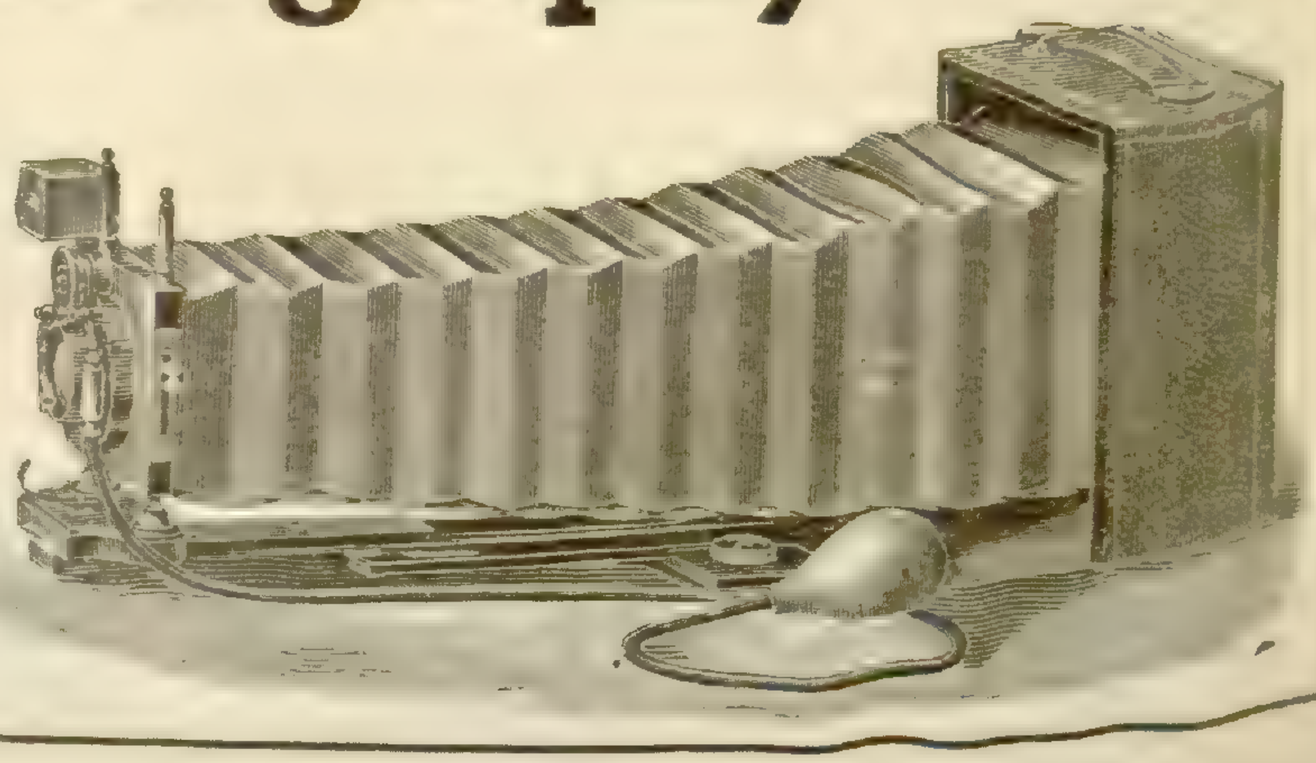

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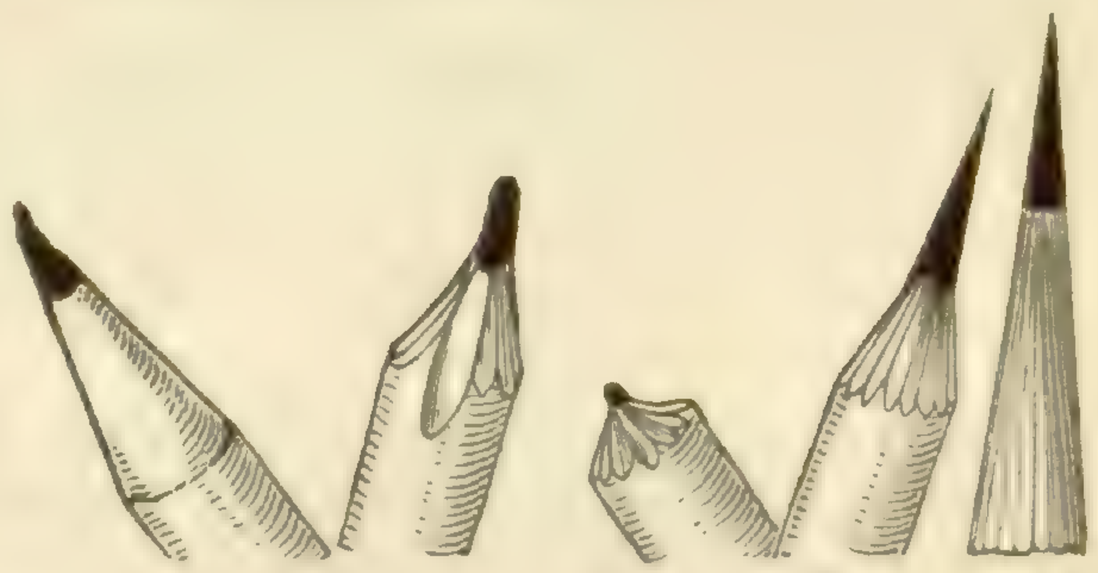

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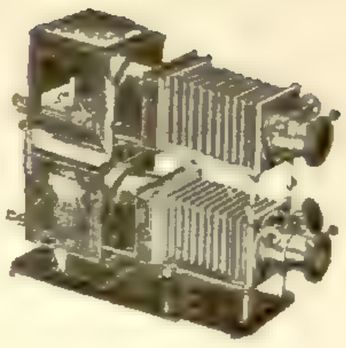

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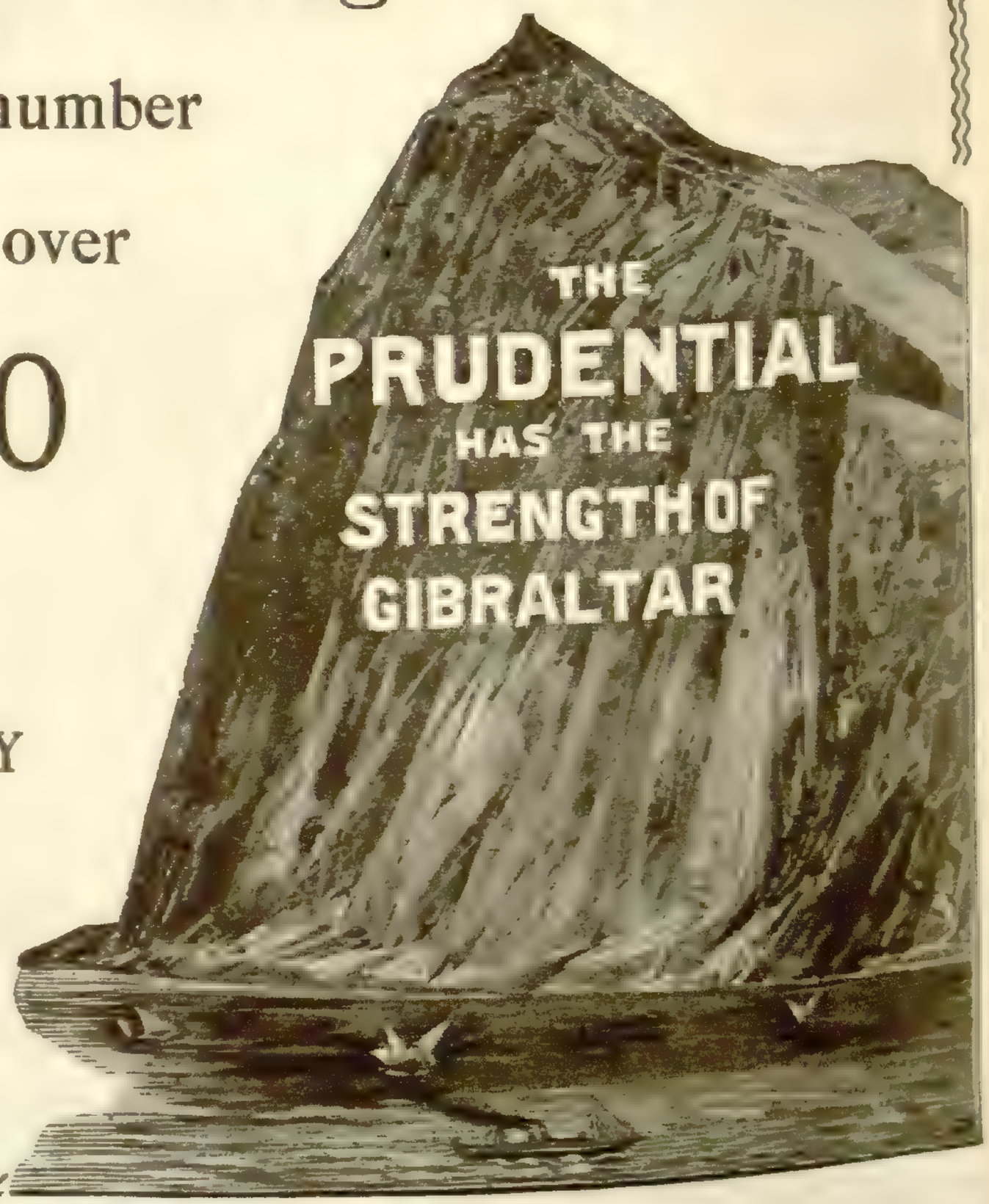


VOLUME XXIX NUMBER 4

BOTANICAL GAZETTE

APRIL, 1900

THE STRUCTURE AND DEVELOPMENT OF THE SPOROPHYLLS AND SPORANGIA OF ISOETES.

CONTRIBUTION FROM THE HULL BOTANICAL LABORATORY.

XVIII.

R. WILSON SMITH.

(WITH PLATES XIII–XX)

FEW plants have excited more interest than Isoetes, a small genus of about fifty species, which has been variously classified, and the histology and development of which have been described in the most contradictory manner. It was with the purpose of obtaining, if possible, some data by which to clear up its homologies and relationships, and especially of examining the foundation of a claim made in recent years of its being the point of contact between monocotyledons and vascular cryptogams that the following investigation was undertaken.

The intention at first was to have the work include not only the reproductive parts of the sporophyte, but also the development of the female gametophyte and of the embryo. But so small a proportion of the spores was found capable of germination that the study of the prothallium had to be abandoned; and my

observations of the embryo agree so closely with those of Professor Campbell (4) that it did not seem worth while to publish any drawings. One difference may be noticed here and this part of the subject may be dismissed at once. Campbell says that but three archegonia are formed at first, and only in case none of these are fertilized do others appear. I have found new archegonia appearing even after three embryos had begun to develop, two of which had made considerable growth. It thus appears that sometimes new archegonia may arise even after fertilization.

The species selected for study were *I. echinospora* and *I. Engelmanni*, the former of which was examined more carefully. The material was collected by Mr. Raynal Dodge, of Newburyport, Mass. Part of it was fixed at once, and part after it had been cultivated for some time in the laboratory. The fixing reagents employed were 1 per cent. chrom-acetic acid, and Flemming's weaker solution. After remaining twenty-four hours in one of these fluids it was washed twenty-four hours in water and transferred through graded alcohols and chloroform or xylol to paraffin. The sections were cut 5, 10, or 15μ in thickness and stained in the ordinary way on the slides. Delafield's hæmatoxylin and erythrosin, safranin and gentian violet, Heidenhain's iron-alum-hæmatoxylin, and cyanin and erythrosin were all used with good results except in the case of the megaspore mother cell.

THE STEM.

The technique which is best adapted to an investigation of the development of the sporangia is not very suitable for an examination of the histology of the stem. Accordingly I have not attempted to make an exhaustive study of the latter, or of the vascular bundles of the leaf. Still the arrangement of the stem tissues is so peculiar that a few remarks will not be out of place. There is probably little variation in this respect in the different species. *I. echinospora* and *I. Engelmanni* agree very closely with *I. lacustris* as figured and described by Farmer (1), whose account is the latest and best dealing with the structure

of the vegetative organs. The center of the stem is occupied by a mass of short spiral and reticulated tracheids interspersed especially near the periphery with less numerous parenchymatous cells. The peripheral parenchyma is not sufficiently aggregated or continuous to form a xylem sheath such as occurs in the leaves. The xylem region is surrounded by a ring of tabular cells of glistening white appearance, thick-walled and empty towards the center but thin-walled towards the outside and more or less banded with incomplete layers of starch-containing cells. The cells are arranged in pretty regular radial rows, whether examined in longitudinal or transverse section. This ring is usually designated the prismatic layer, and very frequently, after Russow (1), the phloem. Russow claimed to have traced a continuity between the prismatic layer and the phloem of the leaf. I have not been able to satisfy myself of any organic continuity, but even did it exist it seems to me very questionable whether that would be a sufficient reason to justify Russow's view. No clearly defined sieve-tubes, the essential elements of the phloem, have ever been found either in the stem or in the leaf; and besides the inner cells of the prismatic zone are known to become secondarily thickened and transformed into xylem tracheids. The cells marked *o* in *fig. 5* are in this process of transformation. Does not this indicate, if not a xylem character, at least the undifferentiated nature of the prismatic cells? A transformation of phloem into xylem would be, to say the least, an anomaly. In view of these difficulties to which may be added another — the relation to the cambium — it seems better to drop this application of the word phloem until its justification shall be established on physiological grounds. A small portion of the prismatic layer is shown in *fig. 5*.

Immediately outside the prismatic layer and indistinguishable from it except in the staining and size of the cells, is a zone of meristem which by its active division gives origin outwardly to an immense mass of cortex, and internally adds slowly to the prismatic layer. This zone is the so-called cambium. Its cells contain deeply staining plasmic contents in addition to starch

(*fig. 5*). Whether or not the dividing cylinder is more than one cell-layer in thickness I could not determine.

The cortex is very bulky and consists throughout of isodiametric parenchymatous cells abundantly filled with starch together with a little oil. The cells undergo no divisions, but as they are forced outward by the activity of the cambium they increase very greatly in size (*figs. 6* and *7*). In this way by the growth of the cells in all directions the cortex expands upwards and downwards as well as outwards, and as a result carries up the older leaves to a height considerably above the stem apex. This is illustrated in *fig. 68*, in which the unbroken lines represent the form which the cortex would take if its cells underwent no enlargement as they are pushed out from the cambium, and the dotted lines the form and dimensions which it actually assumes.

The stem apex lies at the base of the conical depression formed in the manner just explained. In small plants it is distinguishable in longitudinal sections as a slight elevation (*fig. 3*); in older plants it is merely a flattened area between the bases of the young leaves (*fig. 4*).

The method of growth of the apical meristem was first correctly described by Hegelmaier (2). Hofmeister (1) had erroneously ascribed it to the segmentation of an apical cell, having been led to that conclusion probably by too exclusive study of young plants. There is neither an apical cell nor such a group of initials as might result from the division of a rectangular apical cell like that of the Marattiaceæ. Only two or three layers of cells show their meristematic nature by their contents. The superficial layer appears to divide only in an anticlinal direction except when young leaves are about to be formed; but this layer, as Hegelmaier showed, can on no account be regarded as a dermatogen.

Although all the species of Isoetes are perennial, only a small portion of the plant persists from year to year. The roots, the leaves, and the bulky cortex are shed or decay annually, and are as often renewed from the stem apex and the meristematic zone which surrounds the small central permanent cylinder.

THE LEAF AND LIGULE.

In its earliest recognizable form the leaf rudiment seen from above is a crescent-shaped band of meristematic cells, curved about the stem apex. Sections show that it arises from the superficial cells of the stem apex, and is soon pushed up into a low broad mass, highest in the middle and inclined inwards. The ligule appears very early, and the leaf becomes distinguishable into a proximal part somewhat triangular in section and destined to bear the sporangium, and a distal part approximately circular in section and destined to become the chlorophyllous region. In correlation with the rapid development of the sporangium, the growth of the leaf is at first almost confined to the basal region. Compare, *e. g.*, the three leaves shown in *fig. 8*; tranverse sections would show the rapid growth of the basal region in a still greater degree. This region continues to widen as the leaf is pushed outward, by the formation of new leaves and the diametral enlargement of the stem; but longitudinally, except for a slight addition below the sporangium, there is only sufficient growth to accommodate the sporangium, velum, and ligule.

When the sporangium is well under way the region of rapid multiplication and growth of cells is transferred to the part above the ligule. The cells here are arranged with beautiful regularity, and growth is so rapid that this soon becomes the most prominent part of the leaf. The maximum diameter, so far as the number of cells is concerned, is speedily attained, and growth thereafter is only in the longitudinal direction. At first every part of the leaf rudiment is meristematic, but in a short time the apex passes over into permanent tissue. This change into permanent tissue progresses gradually downward until finally the whole leaf is involved. For some time a region of ever narrowing extent above the ligule continues in active division, but there is present no sharply marked or persistent meristematic zone, as seems to be implied in Farmer's account. The leaf is still quite small when all cell divisions have practically ceased, and its further elongation, which may amount to

400 or 500 per cent., is accomplished by the growth of the individual cells.

The formation of the air cavities is interesting, since it is comparable in some respects to the differentiation of trabecular and sporogenous tissue in the sporangium. In a leaf such as is represented in cross section in *fig. 9*, there is yet no sign of the air chambers. Increase of diameter is actively going on and the whole leaf is still meristematic. In the leaf shown in *fig. 10* the position of the future air chambers is indicated by four symmetrically placed groups of cells which have lost most of their contents. The peripheral cells of the leaf, the central cells, and four radiating bands which appear in cross section as spokes arranged in the form of the sign + continue to grow and are distinguishable by their larger more densely filled cells. Stained with Delafield's haematoxylin and erythrosin these cells show deep red cytoplasmic contents and large nuclei in which the red staining predominates; while in the areas which are to become air chambers the cytoplasmic contents have almost entirely disappeared, but the nuclei still retaining their chromatin stain intensely with haematoxylin. When only a nuclear stain is employed, such as iron-alum-haematoxylin, the four non-protoplasmic areas are rendered very prominent by their black nuclei. Longitudinal sections show that the regions which are thus sharply distinct in cross section run lengthwise of the leaf in unbroken bands from just above the ligule nearly to the apex, and there are as yet no air cavities.

The air chambers are formed lysigenously. The growing tissues generate a tension in the empty cells, and as a result these are ruptured irregularly, and small cavities appear, separated by diaphragms or plates of cells extending across from the central to the peripheral growing regions. As the leaf elongates, the air cavities increase in size, while the diaphragms drawn farther and farther apart lose their protoplasm to the surrounding cells. When once this splitting into diaphragms and cavities has occurred, it is not repeated; there remains no meristem in which they may be generated. Occasionally single diaphragms

of unusual thickness may be again ruptured, but no considerable increase in their number ever occurs after their first formation.

It is easy with the low power of the microscope to count the diaphragms in leaves floating upon a little water on a slide. The usual number is from fifty to seventy, and is quite as many in young leaves three fourths of an inch long as in leaves fully formed. It is instructive, too, as proving the absence of a definite meristematic zone, to count the average number of superficial cells which intervene between the diaphragms. In very young leaves this is from three to six or eight throughout the whole length, but in older leaves it is much greater, varying from twelve to twenty in the tip region to forty to sixty in the middle and basal regions, which remain longest in the meristematic condition.

The diaphragms, I think, are quite functionless, and their existence merely incidental to the manner of origin of the air chambers. They are too delicate to serve for mechanical support, which is sufficiently secured by the four longitudinal bands already described. The position of the air chambers and longitudinal bands between them in relation to the axis of the plant is always the same as that indicated in *figs. 10, 11, 44*. Near the ligule the air spaces are less regular, and instead of four of them symmetrically placed we find many irregular ones. Behind the sporangium the dorsal longitudinal band of living cells, and sometimes the two lateral ones, are well marked, but there are no large distinct air spaces. The vascular bundle of the leaf is as characteristic as that of the stem. My observations, referring chiefly to the changes of form of the bundle, were made with the view of discovering whether there is any definite relation between it and the sporangium or the ligule, and whether it presents any evidence that the leaf of Isoetes has been reduced from a more complex type. The leaf trace can first be recognized in the base of the young leaf and in the stem region below it towards the central bundle. The xylem elements are first differentiated, and consist of five or six tracheids grouped into a cylinder and surrounded by a sheath of parenchymatous cells with dense

contents. These parts can be traced later to the corresponding parts of the axial bundle. Behind the sporangium the xylem spreads out into a broad band in which the amount of xylem parenchyma is greatly increased, and the tracheids are in five or six scattered groups. Above the sporangium the xylem contracts again into a cylinder, and lies between the cornua of the ligule base. A more striking change occurs above the ligule where the xylem elements suffer an extreme diminution, there being in that region in *I. echinospora* only a single imperfect central tracheid surrounded by a sheath of parenchyma (*figs. 9, 10*). Occasionally in *I. echinospora*, and usually in *I. Englemanni*, two, sometimes three, other such groups can be traced up the leaf.

The phloem is best represented in the chlorophyll-bearing portion of the leaf. It there consists of two strap-shaped bands on the dorsal side, more or less united by their edges, so as partly to surround the xylem. In less distinct form the phloem may be traced downwards to the region of the central bundle.

The development of the ligule was accurately described by (Hofmeister 1), and also by Hegelmaier (1). The latter refers its origin to more than one cell. Since the former gives few figures, however, and the latter none, I shall again briefly outline the course of growth and illustrate it with a few drawings. The ligule originates from a single large vesicular cell protruding from the ventral face of the leaf rudiment. Provision for its rapid growth is shown in the large size of the nucleus of this cell, and the density of the cytoplasm (*figs. 12, 13*). The first division is always parallel to the face of the leaf (*figs. 14, 15*), and usually the second division is parallel to the first. The ligule of *I. lacustris* is described as passing through a filamentous stage; but in *I. echinospora* and *I. Engelmanni* it is hardly worth while to distinguish such a stage, for the filament never consists of more than three cells. The terminal cell then divides in a vertical plane at right angles to the first wall (*figs. 16, 18*). Other vertical divisions follow until the ligule has become a plate of cells of very regular arrangement. *Figs. 18*

and *19* are median sections of the ligule made tangentially to the face of the leaf. Longitudinal sections are shown in *figs. 26, 27, 28, 33, 35*. Growth in length and breadth continues very rapid, and the ligule soon overtops the leaf (*fig. 8*). For some time it remains a single layer of cells in thickness, but eventually it becomes double throughout most of its extent. The doubling begins in the middle region near the base and extends in all directions, never reaching the apex or margin however, which remain to the last but one layer in thickness (*fig. 21*). The expanded part soon reaches its maximum growth. Not so the foot region; this becomes quite massive and deeply embedded in the tissue of the leaf, especially at the sides which grow upward and downward into two prominent cornua. *Figs. 22–25* may help to explain the form of the base of the ligule. *Fig. 25* is a transverse section of the leaf cutting across the cornua above the main place of union of the ligular and leaf tissues. Sections below it show the cornua connected by a transverse band embedded in the leaf; and sections still lower would show portions of the cornua only. The other figures need no fuller explanation than that accompanying the plates.

Along with the growth of the ligule there comes about a differentiation of the cells composing it. There may be said to be four regions. The base is closely surrounded by a layer of small deeply-staining gland-like cells (*s* in *figs. 22, 38*) which we may call the sheath. It forms a conspicuous layer, everywhere investing the base of the ligule, and becoming continuous with the superficial cells of the leaf. Next to the sheath is an irregular layer or band of large empty cells, the *glossopodium* (*g* in *figs. 22, 38;* see also *figs. 23–25*). The glossopodium appears to form the base of the ligule, but the true base includes the sheath which, as a study of the development shows, is derived from the lowermost cell of the young ligule (*fig. 38*). Above the glossopodium are smaller cells containing protoplasm and forming the greater part of the ligule. The apex and margin of older ligules constitute the fourth region; the cells are

shrunken and contorted, their nuclei broken down, and the cytoplasm disorganized.

A study of the ligule of Isoetes to be complete must be accompanied by a comparative examination of the ligule of Selaginella. With this in view I have studied the origin and growth of the ligule in *S. Martensii* and *S. apus*, and compared my sections with the excellent drawings of Professor Harvey Gibson (2). Professor Farmer (1) has expressed the view that the ligules of Isoetes and Selaginella have little in common except their position and name. I have been led to quite the contrary conclusion, to hold in fact that there is a very close homology between the two. What has appealed most to me, in addition to the position of the organs, is the similarity of the regions of which both are seen to consist. The ligule of Selaginella has a glossopodium of large empty cells, sheathed by a gland-like layer, and shows also two upper regions, one of living and one of disorganizing cells. The two are alike also in the absence of chlorophyll, starch, and intercellular spaces; and both show their embryonic character by passing their maximum of growth before the leaf has reached its greatest functional activity. Differences are to be expected, of course, and are chiefly these: the ligule of Isoetes arises from a single cell, that of Selaginella from a group of cells; and, whereas the ligule of Isoetes is almost from the beginning a conspicuous part of the leaf, that of Selaginella is rather late in making its appearance, no trace of it being discoverable until after the sporangium rudiment is plainly perceptible.

THE SPORANGIUM.

The sporangium has repeatedly been made the object of investigation during the last fifty years. Hofmeister (1) was the first to make a careful study of its origin and development. Though his view that the sporangium can be traced back to a single cell has been discredited by later observers, I hope to show that his error was largely due to his exclusive dependence upon longitudinal sections. Except for his failure to see the true

nature of the sporangium rudiment as a transverse row of cells, his account is surprisingly accurate when the imperfect methods of sectioning and staining of that time are taken into consideration.

According to Hegelmaier (2) and Tschistiakoff (1) the sporogenous tissue is differentiated out of a considerable mass of deep-lying meristem between the epidermis and the vascular bundle.

Goebel (1) agrees substantially with the two preceding authors, but is more explicit in his description. The *Anlage* of the sporangium according to him is a group of cells of the leaf base, chiefly the three upper layers. The outer layer gives rise to the sporangium wall, and the hypodermal layer to the archesporium from which all the spore mother cells, trabeculæ, and tapetum are derived. Goebel's account, as confirmed and restated by Sadebeck (1) in Schenck's *Handbuch der Botanik*, has formed the basis of all the text-book descriptions of the sporangium of Isoetes written since that time.

The latest student in this field is Bower (5), whose description is confirmatory of Goebel's except that he traces the origin of the sporangium to a group of superficial cells. This difference, however, is of the very greatest importance. For whereas the derivation of the archesporium by periclinal divisions of superficial cells is the rule in Pteridophytes, the origin of the sporogenous tissue from a hypodermal layer separated from the beginning from the epidermis is a spermatophyte character. The result of Bower's work then is to put Isoetes in line with other Pteridophytes in respect to the origin of the archesporium.

My own results are in the main confirmatory of Bower's as to the origin of the sporangium, though with variations in minor details which may be due to specific differences (Bower studied *I. lacustris*); but as to the later stages of development, especially of the megasporangium, I cannot make my observations harmonize with any accounts hitherto written.

It will, of course, be apparent, when so many discrepancies appear in the descriptions of different investigators, that the

study must be one which involves considerable technical difficulty. This is attributable (1) to the absence of an elongated axis and internodes and the consequent crowding of the sporophylls, and (2) to the early appearance of the sporangium and the consequent difficulty of distinguishing it from the other meristematic tissues in which it is placed. The kinds of evidence on which I have relied in my interpretations may be stated briefly as follows:

1. Study was made of sporangia whose sporogenous tissue was already distinct and unmistakable. Then by comparisons with successively younger sporophylls the attempt was made to trace the sporangium to its earliest rudiment.

2. A careful comparison was made of sections in the three planes, longitudinal, transverse, and tangential. This involved the waste of a great deal of material. For it will be made clear by a glance at *fig. 4* that sections made longitudinal to the stem could give longitudinal sections of very few young leaves, and oftener than not would fail in this altogether, since the leaves have a spiral arrangement; while, in order to obtain transverse and tangential sections, one must cut obliquely to the stem without possessing any clue by which to determine the proper angle of obliquity.

3. The position of the vascular bundle enables one to determine whether the sections are truly longitudinal, and which of a number of serial longitudinal sections is exactly median. This help is available only after the sporangium is distinctly outlined, and somewhat advanced in development, for in case of very early stages of the sporangium, the vascular bundle has not yet been differentiated.

4. In such early stages one must depend very largely upon the ligule, which in position and outline is so definite, and in manner of growth so regular as to make it of the highest importance in assisting one to orient the sections.

5. The sporogenous tissue is often distinguishable from vegetative tissue by a difference in staining. There are three periods when this difference is most manifest. The superficial

cells which form the earliest rudiment of the sporangium frequently take a distinctive cytoplasmic staining, especially in material fixed in Flemming's solution. It must be confessed that this means of recognizing sporogenous tissue is not so trustworthy as one could wish, for at this period of the leaf's history all the tissues are meristematic, and hence readily susceptible to protoplasmic stains. One who studies the origin of sporangia in Lycopodium or Selaginella meets with the same difficulty in those plants, a difficulty in my experience quite as great in these cases as in Isoetes. When the superficial layer of the sporangium has assumed its character as an epidermis, the deeper lying sporogenous cells are easily distinguishable by stain reactions from the surrounding tissues. At a later period the spore mother cells selected out of the general internal mass of the sporangium become quite distinct on account of their denser contents and more intense staining.

Longitudinal sections of young leaves show no space between the base of the ligule and the stem. At this time there is still an active uplifting of cells above the general stem level, a continuance of the process by which the leaf first emerged. When the ligule has grown sufficiently to contain eight or ten cells in longitudinal section the space below it is occupied by one large cell with dense cytoplasmic contents (*fig. 26*). The next change which takes place is a transverse division of this cell as shown in *figs. 27, 28*. Comparisons of successive serial sections show that the two cells shaded in *fig. 27* form the middle of a group of cells arranged transversely to the leaf. This group of cells, distinguishable in good preparations by their deeper staining and larger nuclei, constitute the rudiment of the sporangium. In order to learn its extent and arrangement recourse must be had to transverse and tangential sections.

Most transverse sections of this early stage of the sporangium show that it is five cells in width. Whether or not these can be traced back to a still smaller number I am in doubt. *Fig. 29* certainly shows an example where the transverse row consists of only three cells, and it is clear that the shaded cells of *fig. 30*

may have had their origin in three similar to those of *fig. 29*. But I have succeeded in getting only two such cases as that of *fig. 29*, one in *I. echinospora* and one in *I. Engelmanni*, and have failed altogether to obtain a tangential view.

Tangential sections of the leaf at this early stage are almost uninterpretable. The face of the leaf is so closely pressed against the back of the next younger one that it is quite impossible in most instances to distinguish the tissues of the two leaves or to determine what is a truly tangential section. That shown in *fig. 31* was such as to admit of certain interpretation. The shaded cells occupy the surface of the leaf and clearly correspond to the group which we have already examined in longitudinal and transverse sections. It is probable that another cell seen in the adjacent section to the left of those figured belongs to the same group, making the total number of cells seven.

It is evident from a comparison of my *figs. 26–28* with *figs. 104–106* of Professor Bower's plates, that the longitudinal growth of the leaf base of *I. lacustris* is much more rapid than that of *I. echinospora;* and his figures though not his text suggest that the six superficial cells which make up the sporangium *Anlage* are derived from not more than three rows and probably from but two. If this suggestion be correct, it would bring Bower's and Hofmeister's accounts, so far as regards longitudinal sections, into harmony with each other, and with the foregoing account of *I. echinospora.*

The young sporangium, situated as it is on the hollow side of the leaf crescent, projects little if at all from the surface. By its rapid growth, however, it soon forms an oval prominence at first wider than long, then nearly circular in surface view, and finally considerably longer than wide. In its development I have not been able to establish any regular order of sequence. Starting from such a beginning as figured in *fig. 26*, it is certain that transverse and longitudinal divisions are the first to occur. Then periclinal walls appear (*fig. 30*). The middle cells of the sporangium rudiment are at first most active in dividing, not only in respect to surface growth, but in periclinal divisions also.

Sections adjacent to that represented in *fig. 31* show three or four hypodermal cells which have been cut off from the middle cells of the group and evidently belong to the same series.

There is at no time a single complete hypodermal layer which may properly be termed an archesporium. For when the middle cells have just completed their periclinal divisions the lateral cells are still undivided, and by the time the lateral cells have undergone their first periclinal division the middle of the sporangium is at least three layers deep. A very good example of this is seen in *fig. 42*, which represents the side of quite a large sporangium.

The growth of the sporangium is carried on most actively by the two or three outer layers of cells, as is evidenced by their large size and deeper staining, and the frequency with which they are found in karyokinesis. The divisions of the superficial layer are by no means limited to those in anticlinal planes, as is usually the case with the external cells of sporangia, but for a long time they continue to add to the inner mass by periclinal divisions. In the sporangium of which *fig. 39* shows a section, as many as eight or ten of the external cells were in the act of periclinal division. Even in so old a sporangium as that shown in *fig. 43* the same process is still in continuance. The cells marked with a cross have evidently been derived from the external layer. Though in older sporangia the additions so made go to form part of the sporangium wall, there can be no question that in the younger sporangia they add to the true sporogenous tissue. The bearing of this fact upon the question of what constitutes an archesporium will be considered further on.

It seems necessary to digress at this point in order to make clear some features in which the preceding account differs from what has been recorded by previous observers. Both Hegelmaier (2) and Tschistiokoff (1) assert that the wall of the sporangium is from the beginning ("von Anfang an gesondert") separated from the inner complex, and emphasize with great distinctness the deep-seated origin of the sporogenous tissue.

Goebel (1) states his approval of Hegelmaier's view, but the occasional periclinal division of the external cells does not escape his notice, though he considers it as merely adding to the thickness of the wall. Bower (5), on the other hand, observed both the superficial origin of the sporangium and the failure of the first periclinal divisions to completely delimit the archesporium.

As already stated, I do not find the outer wall separate from the sporogenous complex from the beginning. On the contrary, it is distinctly active in increasing the dimensions of the sporangium. Ultimately the superficial layer loses some of its protoplasmic contents, and assumes the appearance of an epidermis. It sometimes happens that this separation of a wall layer occurs quite early (*fig. 41*), but oftener it is not till the sporangium has come to consist of many hundred cells. Even then periclinal divisions do not entirely cease.

According to my observations there is no regularity in the arrangement of the cells within the sporangium. The discovery of this was a great surprise to me, for Goebel's statement is very explicit: "Each of the cells composing the archesporium has an independent growth," and in this he has been corroborated by Sadebeck and Farmer. Bower has not traced the history of the sporangium with any fullness; he merely states that his results are confirmatory of Goebel's and his figures certainly convey the impression that each cell of the archesporium has an independent growth. But he has made use of the same style of drawing in representing the sporangia of other genera (Lycopodium, Selaginella, Equisetum), in which no such claim is made. In view of my own observations and of Bower's drawings, it is difficult to know just how much is meant by the phrase "independent growth."

In the case of bryophyte antheridia the primary spermatogenous cells are clearly distinguishable throughout the whole development of the antheridium, although each may become divided up into a hundred or more sperm mother cells. The individuality of the original cells is marked in several ways:

their outer walls remain straight and become thicker than those which subsequently appear within them; and the incomplete separation of the derivatives of any single primary sperm cell from one another and their complete separation from those of other primary cells are shown by their dividing concurrently. I have frequently observed in the antheridia of Polytrichum, Porella, Marchantia, and Asterella that all the cells derived from one of the primary sperm cells enter into karyokinesis together, finish their division, and enter into the resting condition together, quite independently of what may be going on in the derivatives of other primary cells. In such cases it is quite proper to speak of an independent growth; for the separation and isolation of each group by thickened walls are sufficient to insure a simultaneous exposure and obedience of all the cells to the physiological stimulus which induces karyokinesis.

Are there any indications of such independent growth in the sporangium of Isoetes? I can find none, either in the arrangement of the tissues or in the presence of thickened walls which mark the boundaries of the original archesporial cells, or in the simultaneous entrance of the cells of each group into the phases of division. All the mature cell walls of a growing sporangium are of equal thickness; and in marked contrast to what is seen in the leaves there is no regularity of stratification or lining-up of the cells. I am forced to conclude that the sporangium of Isoetes (at least of *I. echinospora* and *I. Engelmanni*), just as the microsporangium of angiosperms, grows as a unit and not as a number of individual segments.

Before continuing the subject of the development of the sporangium it will be convenient to consider the formation of the velum. The velum makes its appearance very early in the history of the sporangium, almost as soon in fact as the first periclinal divisions of the superficial cells. It is formed immediately below the ligule. Hofmeister (1) says: "Of the two cells into which by a transverse septum the cell underneath the place of insertion of the ligule is divided the upper one becomes the primary cell of the velum and the lower the primary mother cell

of the sporangium." It has already been said that Hofmeister was in error because of failure to notice the lateral extension of the sporangium rudiment. Even allowing for this, however, I am not able to agree fully with his account. It appears rather that the upper tier of cells while giving rise to the velum makes some additions at the same time to the sporangium. In other words, the velum is a sterilized portion of the sporangium. Some sections seem to admit of this interpretation only, though others, such as *fig. 32*, are not unfavorable to the view that the separation of velum and sporangium proper is accomplished by the first transverse division of the sporangium rudiment.

Early stages of the velum may be seen in *figs. 32–36;* it is at this time a transverse row of slightly projecting cells. Its cells soon become comparatively empty, contrasting strongly with the young sporangium. Growth is very rapid and in an upward oblique direction; in some cases there is a tendency to a downward growth also, such as obtains among terrestrial species.

The velum reaches its full size much sooner than the sporangium, and is not affected by the changes which determine the character of the latter. The cells of the interior become large and lose their contents; those of the inner surface layer—that adjacent to the sporangium—are smaller and more regular in size and outline, and have a semi-glandular appearance. In many species of Isoetes many of the cell walls of the velum and of the leaf region adjoining the ligule become lignified and take on spiral and annular thickenings. *I. echinospora* and *I. Engelmanni* offer no exception in this respect, the thickenings being much more pronounced in the latter species. The change first appears in proximity to the ligule, and spreads thence into the remoter parts of the velum and of the leaf. The thickened cells never have any connection with the vascular bundle (*figs. 23, 24*).

FURTHER DEVELOPMENT OF THE MICROSPORANGIUM.

In origin the two kinds of sporangia are identical, and for a considerable period of their development they exhibit no

observable difference. The general statement of the text-books, following Goebel and Sadebeck, is that they follow the same course of development only so far as the formation of the archesporium, and thereafter may be distinguished by their manner of growth. It is said that in the megasporangium certain archesporial cells divide only by periclinal walls, but in the microsporangium all the archesporial cells divide both anticlinally and periclinally, and that in this respect the two are distinguishable from the archesporial stage on. Such is not the case in the forms which I have studied. In these all the archesporial cells, whether of megasporangium or microsporangium, undergo divisions in all directions, and the similarity of the two kinds of sporangia continues much beyond the archesporial stage. Not only do they agree in origin, but up to a time when they are eight or ten cells deep, they agree absolutely in manner of growth, and exhibit no histological features by which one may determine whether a given sporangium will bear microspores or megaspores.

As an example, consider the sporangium of which *fig. 43* represents a section. It had advanced so far beyond the archesporial stage as to contain about 8000 cells. From the position of its sporophyll we may infer it was destined to become a megasporangium. But there is nothing in the arrangement or character of the cells or in their mode of division to warrant that prediction, or to enable us to say such a group of cells will become a trabecula, and such a group will produce spores. It has the characters neither of a megasporangium nor of a microsporangium, but is as yet quite undifferentiated.

The first changes which occur to mark the microsporangium are those which lead to the differentiation of the spore mother cells from the trabeculæ, sporangium wall, and tapetum. Previously there has been no essential difference in the cells as to size, form, or contents, excepting the external layer. But when the sporangium is approaching a limit of cell multiplication, that is, when the number of cells is 15,000–20,000, certain regions begin to lose their power of division and reaction to stains, while

other regions become more active in division and more deeply stainable. The former may be called the sterile regions, since they form the walls, trabeculæ, and tapetum, and the latter the fertile region, since they give rise to the spores. Even in unstained sections the difference is noticeable as one of relative abundance of protoplasmic contents.

At first it is difficult to see clearly the limits of the regions or to make out their arrangement. But in older sporangia they are seen to be disposed in irregular bands extending from the base of the sporangium outwards to the wall. The published drawings, and unfortunately in some cases the written description also, are calculated to convey an erroneous idea of the trabeculæ. They are not partitions, but, though irregular in outline and frequently branched and anastomosed, are comparable rather to pillars. It is accordingly incorrect to speak of the sporangium as chambered, for the fertile cells are not segregated into loculi, but form a continuous mass pierced here and there by the trabeculæ. It is hoped that *figs. 44–47* will make the relations of the trabeculæ clear. The shaded portions of these drawings represent the fertile regions, and the unshaded portions the trabeculæ and walls. The continuity of the sporogenous mass is clearly seen in the tangential section (*fig. 46*).

A more detailed account of the development of the microsporangium will now be given. *Fig. 48* shows a small portion of a microsporangium in which the differentiation into sterile and fertile regions has just begun. The fertile cells stain deeply and are still rapidly multiplying, as is evidenced by the many karyokinetic figures. The sterile cells have almost entirely ceased divisions, though here and there a dividing cell may be found. It is important to notice that the one character in which the two regions differ is in the relative abundance of protoplasm, the fertile cells being densely filled with deeply staining cytoplasm, while the cytoplasm of the sterile cells is beautifully vacuolated. In all other respects the cells of the two regions are essentially alike. They are not markedly different in size,

or in the size and appearance of their nuclei, nor is there anything in their arrangement to suggest a difference in their origin or growth. In fact, as Professor Bower has pointed out, there is here a most excellent illustration of the sterilization of sporogenous tissue.

The trabeculæ at this age show about 15–25 cells in cross-section (tangential section of the sporangium), and are more or less cylindrical. There is as yet no tapetum. Towards the outer and inner sides of the sporangium the trabeculæ are continuous with about three layers of cells which form the sporangium wall (*fig. 49*). That the trabeculæ and walls are of the same nature, both being the result of sterilization of potentially sporogenous tissue, is proved not only by the similarity of their cells, and their passing uninterruptedly into one another, but also by their relation to the tapetum, which is formed out of the layer that lies next to the spore mother cells.

The inner cells of the trabeculæ, those which become the trabeculæ proper (*i. e.*, exclusive of the tapetum), are at first isodiametric and in no way different from the outer ones. But while the latter are undergoing a transformation into tapetum, the former undergo changes which are dependent on the growth of the sporangium. As the dimensions of the sporangium increase — a change which goes on rapidly at the period when the sporogenous cells are multiplying — the trabeculæ are necessarily lengthened. This is accomplished, not by division of the cells, but merely by their elongation. At the same time they suffer a lateral compression from the growing sporogenous cells and become flattened (*fig. 50*). The tabular form of the cells doubtless furnishes the ground for the common view, which ascribes the form of the cells to the direction of their division planes. Such a view is incorrect, however, for divisions have entirely ceased in this region before the elongated form of the cells is attained. The shape of the cells is easily accounted for by their growth in the one direction possible for them while yielding to the pressure of the turgescent mother cells.

In this connection it may be remarked that with the possible exception of the tapetum all the cells of the sporangium, after

losing their power of division, enter upon a period of growth which is quite comparable to that occurring in vegetative meristems. The difference in size of the sporangia represented by *figs. 43* and *63*, which are drawn under the same magnification, is due partly, it is true, to increase of the number of cells, but a glance at the two figures shows there has been also a decided growth of the individual cells.

Accompanying the modification of the trabecular cells, there is a change of form of their nuclei. These become first elongated and oval (*fig. 50*), and finally spindle-shaped, suggestive of the changes which attend the development of the vascular strand out of the tissues of a growing point. Instances of much greater elongation than that shown in *fig. 51* are frequently met with, though in other cases the changes are comparatively slight. The nuclei at this time are relatively large and prominent, and appear to form the center of aggregation of what little cytoplasm still remains in the trabecular cells. In old sporangia the cells of the trabeculæ are nearly or quite empty, and much compressed.

Bower has discussed the function of the trabeculæ. They may serve for mechanical support of the sporangium, or to afford a larger nutritive surface, or, since the two functions are not incompatible, for both. The relation of the trabeculæ to the base of the sporangium where it is closest to the vascular bundle, and the resemblance of the nuclei to those of plerome regions in general, suggested to me that the trabeculæ might be the channels through which nutriment is supplied to the spores; but the suggestion is not borne out by observation. It is clear that in a hydrophytic plant no elaborate apparatus is needed to provide the sporangium with water, which can easily enter directly from the outside; and an examination of my sections shows that the organized food stuffs, such as starch and oil, pass to the spores through the inner wall of the sporangium, and not through the trabeculæ.

The tapetum, as already stated, is organized out of that layer of the sterile cells, whether of wall or trabeculæ, which is in contact with the fertile cells. At a stage between those shown in *figs. 45*

and *50*, the cells of this layer multiply rapidly. They are frequently found in mitotic division, with the axis of the spindle always perpendicular to the surface of the trabeculæ or sporangium wall. Divisions may still go on here after the spore mother cells have reached maturity, and the changes of the trabeculæ are nearly complete. In this way the tapetal cells become very numerous, but reduced in size. They form but a single layer except in limited areas, where a doubling may sometimes occur.

At first the tapetum is not deeply stained (*fig. 50*), but as the spore mother cells prepare for their tetrad division, the tapetal contents increase in density, and they continue to do so until they surpass young spores in this respect.

From what has been said, and from *figs. 47*, etc., it will be understood that the tapetum completely invests the trabeculæ and sporangium wall, forming a lining layer everywhere between the spore mother cells and the sterile regions. It is a persistent layer, and in this respect is to be contrasted with that of most ferns and angiosperms. In these latter the walls of the tapetum break down and are dissolved, the cells become disorganized, and their materials, mingling with the other contents of the sporangium, are used to nourish the mother cells or young spores. In Isoetes, however, as in Lycopodium and Selaginella, no such disorganization of the tapetum occurs. Its cells do not fall apart and its walls are not absorbed. In old sporangia it is still recognizable, though often its contents have been lost and the walls are pushed nearly together.

Probably the tapetum can best be regarded as a gland or layer of glandular cells. If so, the manner of action in a persistent tapetum, such as that of Isoetes, Lycopodium, and Selaginella, must be quite different from what it is in a tapetum which is regularly disorganized and absorbed. In the one case the nutrient substances secreted by the cells must be passed on through the walls into the cavity in which the young cells are growing. In the other case there can be little or no passing of nutrient substances through the walls, but at the proper time the

secreted materials are rendered available by the total collapse of the cells.

In many plants also, especially in those in which the tapetum undergoes complete disorganization, it is common for the tapetal cells to become multinucleate, the division of the nuclei being sometimes accomplished by karyokinesis, but mostly by amitosis. The cells of the tapetum of Isoetes, in this respect again agreeing with Lycopodium and Selaginella, are uniformly uninucleate.

In almost every sporangium examined the number of layers of cells outside the fertile regions when they first become distinct is three. In a very few cases there were four layers. As already shown, the innermost of these becomes tapetum. Of the other two layers, one, apparently the hypodermal, usually undergoes division, so that the wall region ultimately consists of three layers outside the tapetum.

At the base of the sporangium, between it and the vascular bundle, are a few layers of cells which may be regarded as the inner wall of the sporangium. The exact origin of these I have not been able to make out. Whether, like the outer wall, they are derived from the sterilization of sporogenous tissue, or whether they are derived from the tissues underlying the original archesporium, I cannot say. It is always difficult in all sporangia except the very youngest to define the exact inner limits. Between the vascular bundle and the three or four outer layers where growth and division are most actively carried on, there is a mass of small cells staining deeply. Such a section as *fig. 38* makes it probable that all the tissues between the parenchymatous sheath of the xylem and the outside arises from the sporangium *Anlage*, and that therefore the inner wall arises also by sterilization.

The formation of the microspores in Isoetes takes place in much the same way as in other vascular plants. After the fertile regions have ceased their cell divisions, the cells and their nuclei pass through a period of rest and enlargement. The nuclei especially increase in size and become rich in chromatin. At the same time the cytoplasm remains dense and never

shows the vacuolated appearance of the sterile cells. Shortly afterwards the mother cells break away from the tapetum, which from this time on gains in density and apparent activity. The mother cells, at first in a continuous mass, soon break up into smaller and smaller groups of cells by the enlargement of the cavity in which they float. Finally the individual cells fall apart and round up, and pass rapidly through the two divisions by which the microspores are formed.

No attempt was made to follow closely the cytology of these divisions because it was found impossible to make any satisfactory observations on the corresponding divisions of the megaspore mother cells. The following notes may however be of interest. The achromatic figures appear to have a polycentric origin, and the chromatin passes through a synapsis stage. All the nuclei make their preparation for division and begin to divide almost simultaneously, and this notwithstanding their immense number. It is possible to find a better series of karyokinetic figures in a single sporangium of many ferns, where there are but sixteen mother cells, than in an Isoetes microsporangium where the mother cells number three or four times as many thousand. This I think may be regarded as an additional proof of the growth of the sporangium as a unit, and not as an aggregation of segments.

In the majority of cases the two divisions are of the type which is characteristic of cycads and monocotyledons, and has been called "successive;" that is, the first division of the nucleus is followed by the formation of a cell wall before the immediately following division of the daughter nuclei (*fig. 53*). The spores in this case are bilateral and may have their nuclei in one plane or in two planes at right angles to each other. But it is not at all infrequent to find the divisions of the simultaneous type; that is, the first division of the nucleus is not attended by cell division, but before a wall is formed between the daughter cells each new nucleus begins its second division (*fig. 54*). In this case the spores may be of the bilateral type, as in *fig. 55 a* and *b*, or they may be tetrahedral as in *fig. 55 c*. Much

diversity may be found within a single sporangium. *Figs. 53 a, b, c,* and *54 a, b, c,* were all taken from the same section of the same sporangium. Probably the variation in this respect is not of great importance except as indicating that the divisions of Isoetes have not acquired so definite and settled a character as those of most other plants.

Although the nuclei of the young spores may arrange themselves in typical tetrahedral fashion, there is an important difference between their relation here and in the tetrahedral divisions of dicotyledons, Lycopodium, etc. In these it is well known that all four nuclei (of such a stage as *fig. 54*) become connected by spindle fibers, and that the walls separating the spores are formed in connection with the thickening of the cell plates of the six spindles. In spite of careful search I have been unable to find in Isoetes any such sextuple spindles. The daughter nuclei are connected only in pairs, as in *fig. 53* or *54*. In what way the spore walls originate in such cases I cannot conjecture. It seems certain they are not formed in connection with the achromatic figures, unless it is possible that the cell plate, which is always present in the first division, may make its influence felt later on, and ultimately serve as the basis of the wall.

The young tetrads soon fall apart, and the individual spores lose their angularity and round up, still retaining traces, however, of the bilateral shape impressed upon them by their manner of origin. When once the permanent form is assumed there is little further increase of size. The mature spores of *fig. 56* are little larger, it will be seen, than the newly formed spores of *fig. 51*.

An interesting phenomenon in connection with the microspores is the extreme smallness of their nuclei in comparison with those of the mother cells. One would naturally expect the relative volumes to be about 1 : 4, or the relative diameters to be about 3 : 5 (since $\sqrt[3]{\frac{1}{4}} = \frac{3}{5}$ nearly). But the volume of the microspore nucleus is really no more than one twelfth of this estimate; or to express the comparison in another way, it would need the nuclei of fifty microspores combined to equal the

volume of one mother cell nucleus. Very likely similar reductions in the volume of the microspore nuclei occur during the tetrad division of other plants, but I have not seen any other case where the disparity of size is so great, nor do I remember to have read any record of such a reduction.

The number of spores formed within a microsporangium is enormous—much greater than in any other living plant. In some species it is said to exceed a million. But the largest number I have found in *I. echinospora* is 300,000. My estimates place the average number from 150,000 to 250,000.

As is well known, no provision is made for the dehiscence of the sporangium wall. The spores are set free only by the decay of the tissues enclosing them.

FURTHER DEVELOPMENT OF THE MEGASPORANGIUM.

My observations on the development of the megasporangium differ very much from those of previous investigators, so very much, indeed, that I would be loath to present them at all had I not confirmed them again and again by long and careful study. These differences are concerned not only with the origin of the archesporium and early growth of the sporangium, which have been already spoken of, but they involve also the manner of selection of the mother cells and the origin and behavior of the tapetum. A discussion of the points at issue will be reserved until the general history of the megasporangium has been considered.

One of the first megasporangia which I sectioned presented the appearance shown diagrammatically in *fig. 67*. The two large cells *M* and *M* are evidently megaspore mother cells, but what is the group of cells *a*, corresponding to them in outline and position? It consists of six cells in all, three in the section under examination, and three others in the adjacent section. A little search discovered other similar groups of a variable number of cells, sometimes but two or three, often five or six. If the number had been constantly four the groups might have been regarded as spores resulting from a precocious division of

the mother cells. But that explanation being precluded it became necessary to determine their relation to the single large mother cells, and to learn their later and earlier history. In attempting to do so I have become convinced that a very large number of cells are potentially megaspore mother cells, that a considerable number of these make a start to differentiate themselves fully from the sterile cells, but that comparatively few are finally successful in reaching the large size and well-nourished condition necessary for the production of megaspores.

The changes which first distinguish the megasporangium occur relatively earlier than those which mark the microsporangium. In the latter, as we have seen, the first change is the separation of certain sterile regions from the fertile cells as indicated by a difference in cell contents. In the former, however, changes occur at a considerable time before there is any possibility of distinguishing the trabeculæ. When the megasporangium has reached a stage of development considerably more advanced than that shown in *fig. 43*, a change is discernible in many of the cells which form the third and fourth layers approximately. The whole sporangium has at this time entered upon the period of enlargement due to the growth of the individual cells. But in *fig. 63* it is clear that certain cells have greatly outgrown their fellows. Their well-nourished condition is attested by the density of their cytoplasm and their large nuclei, which contain many nucleoli. All these enlarged cells are engaged in the struggle to become mother cells. Which and how many will be successful will probably depend upon their holding an advantageous position with respect to the supply of nutriment, perhaps also to their having obtained an earlier start.

It does not always happen that a considerable group of cells enlarge together. Indeed, it is a comparatively rare case when all the cells of the third and fourth layers enlarge to any considerable extent. Sometimes the enlarging cells are in more or less isolated groups separated by cells of ordinary size. *Fig. 64* shows such a group of cells, taken from the side of a sporangium.

Quite often, too, it happens that one cell gets the advantage almost from the beginning. But it may be stated as the rule that there is a selection and partial enlargement of many more cells than can ultimately become mother cells, and these enlarging cells belong mostly to the third and fourth layers of the sporangium, either extending continuously across the sporangium or occurring in groups separated by ordinary cells. That this condition is associated with the selection of megaspore mother cells is proved, I think, by the fact that enlarging cells, comparable to those of *fig. 63*, are never found in the sporangia formed late in the season, that is, in those which are to bear microspores.

What becomes of the defeated cells? This is a difficult question to answer, for since there is so much variation in the early condition of the megasporangium it is impossible when examining one of the later stages to tell just what the antecedent conditions in that sporangium may have been. From the frequency with which karyokinetic figures appear in the cells surrounding the nearly mature megaspore mother cells, it seems pretty certain that the cells which have been left behind in the struggle simply divide until their products have the general size and appearance of the other cells of the sporangium. If the enlargement has not gone very far the cells retain their angular configuration; if it has gone further the cells may round up while exerting a considerable pressure on those adjacent. So I interpret the group *c* in *fig. 67*.

Fig. 66 will furnish a good illustration of the behavior of the unsuccessful mother cells, although no single section can be so convincing as a series of them. The tissues are somewhat contracted, but this defect does not hide the rounded form of certain groups of cells, and their marked resemblance, except in being multicellular, to the mother cells. The section contains but one fertile mother cell, the one labeled *m*. One other is situated in the opposite end of the sporangium, just beyond the limit of the figure. The cell *a* is undergoing division, the mitotic figure being seen in the adjacent section. An interesting fact

which goes far to explain the division of the groups *b*, *b*, is the occurrence in adjacent sections of larger undivided cells (fertile mother cells), similar to *m*, and so situated as to be almost or quite in contact with the dividing groups. Their proximity accounts for the failure of the groups *b*, *b*, to produce spores. Some of the smaller and less rounded groups probably represent mother cells which suffered an early defeat, while the larger groups represent those which held out almost to the last. Such cases as these, which can be easily duplicated in rapidly growing sporangia of the right age, are conclusive, it seems to me, when considered in conjunction with the manner of growth of the sporangium, to show that the fertile mother cells are selected by their advantageous environment and not by any strict morphological position.

The fertile mother cells increase enormously in size before dividing into spores. Their nuclei maintain a proportionate growth, and their cytoplasm remains dense though not homogeneous, and frequently contains grains of starchy matter and drops of oil.

Notwithstanding the large size of the mother cells and of their nuclei I was unable to make any detailed study of their division. About the time when division occurs, the cells seem to be peculiarly liable to suffer plasmolysis, for under the action of the fixing agent they are contracted to a mere fraction of their proper volume. When sectioned in this condition they are seen to lie free in large cavities which presumably they filled completely when living, and they stain so intensely that it is impossible to make out any details of the karyokinetic process. I have not once had the good fortune to see karyokinesis in an uncontracted megaspore mother cell, although the corresponding phase of the microsporangium offers no technical obstructions to cytological study. The liability of the megaspore mother cells to suffer contraction in the process of fixation was noticed by Kienitz-Gerloff (1) and other investigators; it is possibly associated with the entrance of the nuclei into the synapsis stage.

The young megaspores almost invariably have the tetrahedral arrangement, as in *fig. 59*. Occasionally the bilateral arrangement is found, in which case the divisions so far as observed are successive (*figs. 60, 61*).

The further growth of the megaspores, the manner in which their walls are laid down, and the storing of reserve material, were not investigated.

The arrangement and subsequent development of the trabeculæ and tapetum of the megasporangium offer, as is to be expected, a rather close homology to what is seen in the microsporangium. The trabeculæ are formed out of the same kind of cells as compose all the other parts of the young sporangium. I do not discover any grounds for considering them the product of a peculiar kind of growth. They are altogether unrecognizable in the young sporangium, and their position when first outlined seems to be determined by that of the mother cells. Not until these have been selected and considerably enlarged is it possible to distinguish the trabeculæ, which then appear as feebly-staining bands extending from front to back across the sporangium midway between the fertile cells.

The cells of the trabeculæ proper undergo the same process of elongation and flattening, attended by elongation of their nuclei, that has been described as occurring in the microsporangium. The only noticeable difference is that in the megasporangium the trabeculæ are relatively fewer in number and more massive. For example, in one case, an exceptional one, I counted 400 cells in a cross section of a trabecula, whereas in a microsporangium the number of cells in a cross section of a trabecula rarely exceed fifty, and is oftener under twenty-five. This is only another way of saying that the process of steriliza tion has gone much further in the megasporangium than in the microsporangium. The total mass of the megaspore mother cell in a sporangium is only a small fraction of that of the combined microspore mother cells, though doubtless the total volume of the mature spores in the two cases is about equal.

The tapetum is formed in this case also out of those layers of the sterile cells which border upon the fertile cells. No doubt a considerable part of it is derived from the unsuccessful mother cells; but as these are the homologues of the trabecular cells of the microsporangium, being merely sterile sporogenous cells, the homology of tapetum and trabeculæ in the two sporangia is complete. The only difference which it is necessary to notice is the greater abundance of the tapetum in the megasporangium. Instead of being a single layer it is several layers in thickness (*figs. 57, 58*), and often projects into the sporangial cavity in the form of irregular papillæ, especially from the base of the sporangium. A rounding up of the cells immediately about the megaspore mother cells, such as is described and figured by Goebel, I was never able to find.

Though the megaspore mother cells do not lie in contact with one another as the microspore mother cells do, but are isolated in groups of one or sometimes two, the cavities in which they lie become continuous in the older sporangia. This is brought about by a very great enlargement of the cavities after the formation of the spores. The enlargement seems to be due to turgescence, induced probably by the osmotic activity of the substances surrounding the spores. It cannot be accounted for by mere growth of the wall cells, nor by that of the young spores, for these do not completely fill the cavities. I have computed the enlargement of the megasporangium after all cell divisions have ceased to amount to an increase of three or four times in volume. A similar change of size, though less in extent, occurs in the microsporangium.

If the preceding account of the development of the sporangia, especially of the megasporangia, be compared with the account given by Goebel (1) and Sadebeck (1), it will be seen that the differences are considerable, and of much theoretical importance. According to these writers certain cells of the archesporium divide only by the periclinal walls which serve to cut off the primary tapetal cells. In these no anticlinal divisions occur. One cell of each of the rows formed in this manner.

apparently the innermost one, though that point is not made clear in the descriptions, becomes the megaspore mother cell.[1] In certain other archesporial cells divisions take place in all planes, but more particularly in the anticlinal direction. The products of these latter cells give rise to the trabeculæ. Vines in his text-book gives nearly the same description, but says that the archesporial cell from which the megaspore mother cell arises undergoes but a single division.

If the assertion be correct that certain archesporial cells develop only into trabeculæ and certain others only into mother cells and tapetum, it is clear that there must be two categories of archesporial cells, one set destined to become sterile, the other to become fertile; and these, although indistinguishable in appearance and size, are quite unlike in their mode of division and growth and in the ultimate fate of their derivatives. It is impossible, too, to escape the inference that the megaspore mother cells are already determined in position and number when the sporangium has got no further in its development than to the differentiation of an archesporium. Further, the sporangium must be regarded as compound, each fertile archesporial cell representing a separate sporangium, and each sterile one an imperfect wall. These conclusions, which I think are logical and necessary deductions from Goebel's description, are all inconsistent with the development of the sporangium as I have found it in *I. echinospora*.

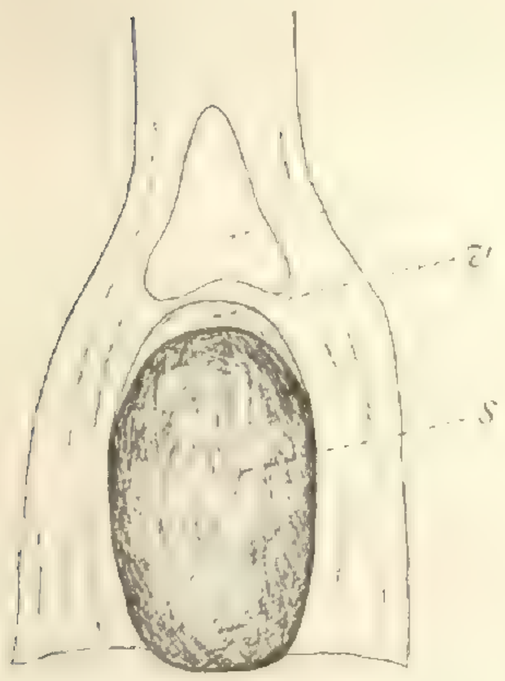
In order to bring out the points of contrast more clearly I will summarize them. I do not find any difference among the archesporial cells either in manner of development or of growth. I find no flattened tapetal cells overlying the megaspore mother cells. I find no grounds whatever for the assertion that each archesporial cell follows an independent growth, or that each megaspore mother cell represents one archesporial cell. I do not even find a single definite hypodermal archesporium which can stand as the starting point of the inferences above enumerated. On the other hand, I find the derivatives of all

[1] See, however, SCHENCK's Handbuch 3 : 392.

the archesporial cells dividing in various planes, and blending indistinguishably. The sporangium is single, not multiple, and the megaspore mother cells are not morphologically predetermined but are physiologically selected from among a large number of potentially sporogenous cells.

Though the certainty of the matter must depend upon observation, it may be pointed out that the number of megaspores has a bearing upon the question. A megasporangium contains from 150 to 250 megaspores. If we take 200 as the average, it represents fifty mother cells, that is, according to the current view, fifty archesporial cells. To this we must add at least fifty others for the trabeculæ, giving a total of one hundred archesporial cells. It does not need a very careful examination of *I. echinospora* to demonstrate the impossibility of there being so large an archesporium, for when the sporangium has a superficies of one hundred cells it is far past the archesporial stage. It is, I think, absolutely certain that each archesporial cell gives rise to several megaspore mother cells, as well as to trabeculæ and tapetum. In the microsporangium, too, the trabeculæ alone outnumber the archesporial cells (*cf. figs. 31, 46*); and their extreme irregularity and frequent branching and anastomosis make their origin each from a single cell exceedingly improbable.

[*To be concluded.*]



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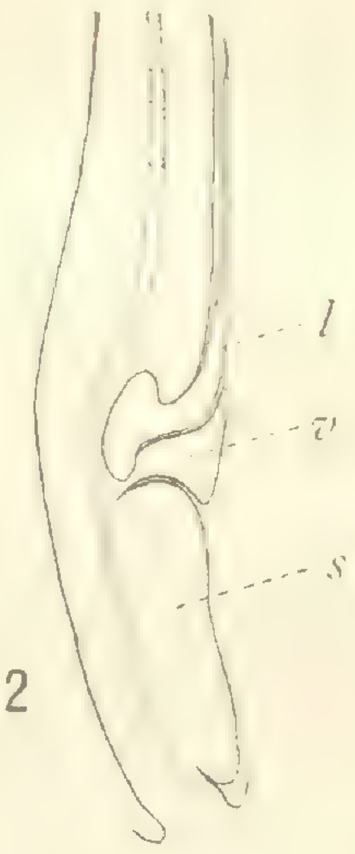

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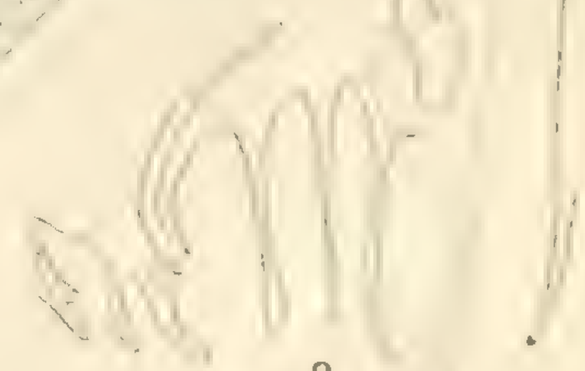

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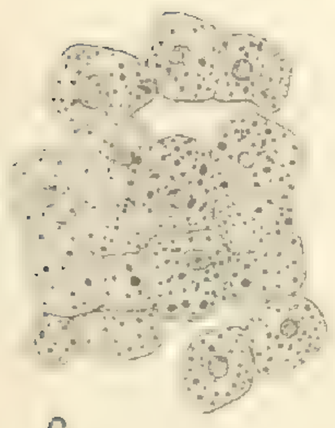

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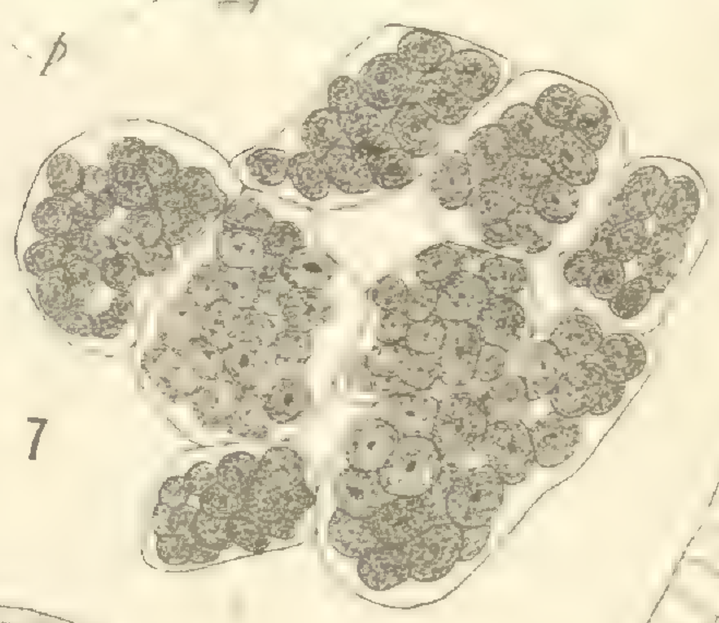

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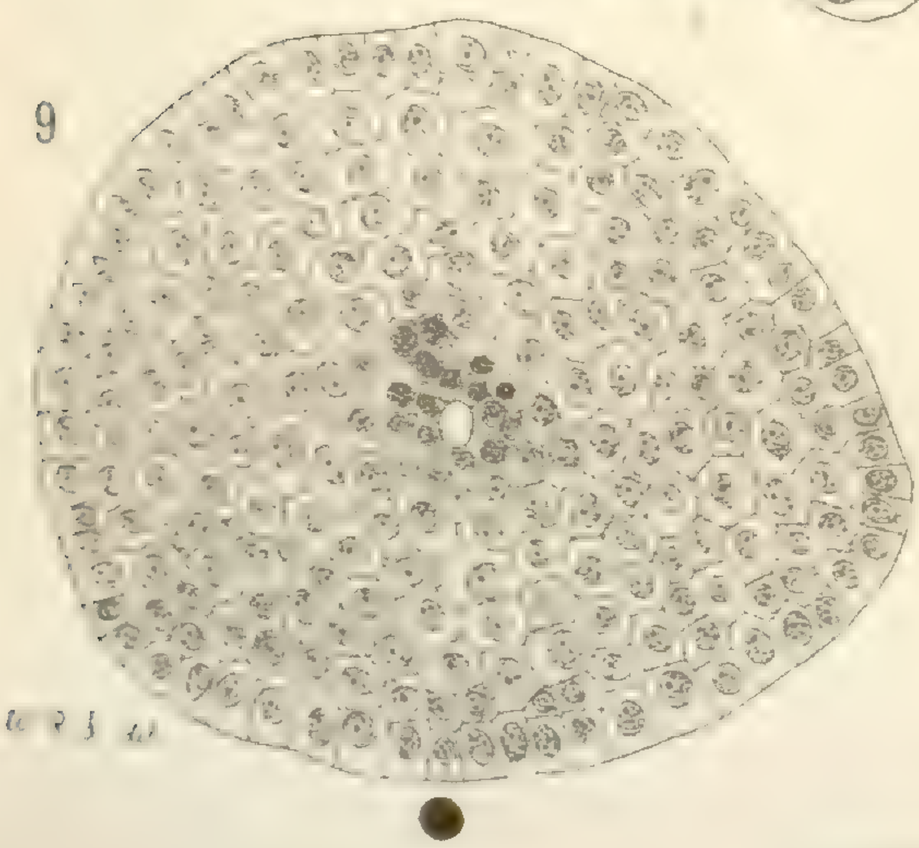

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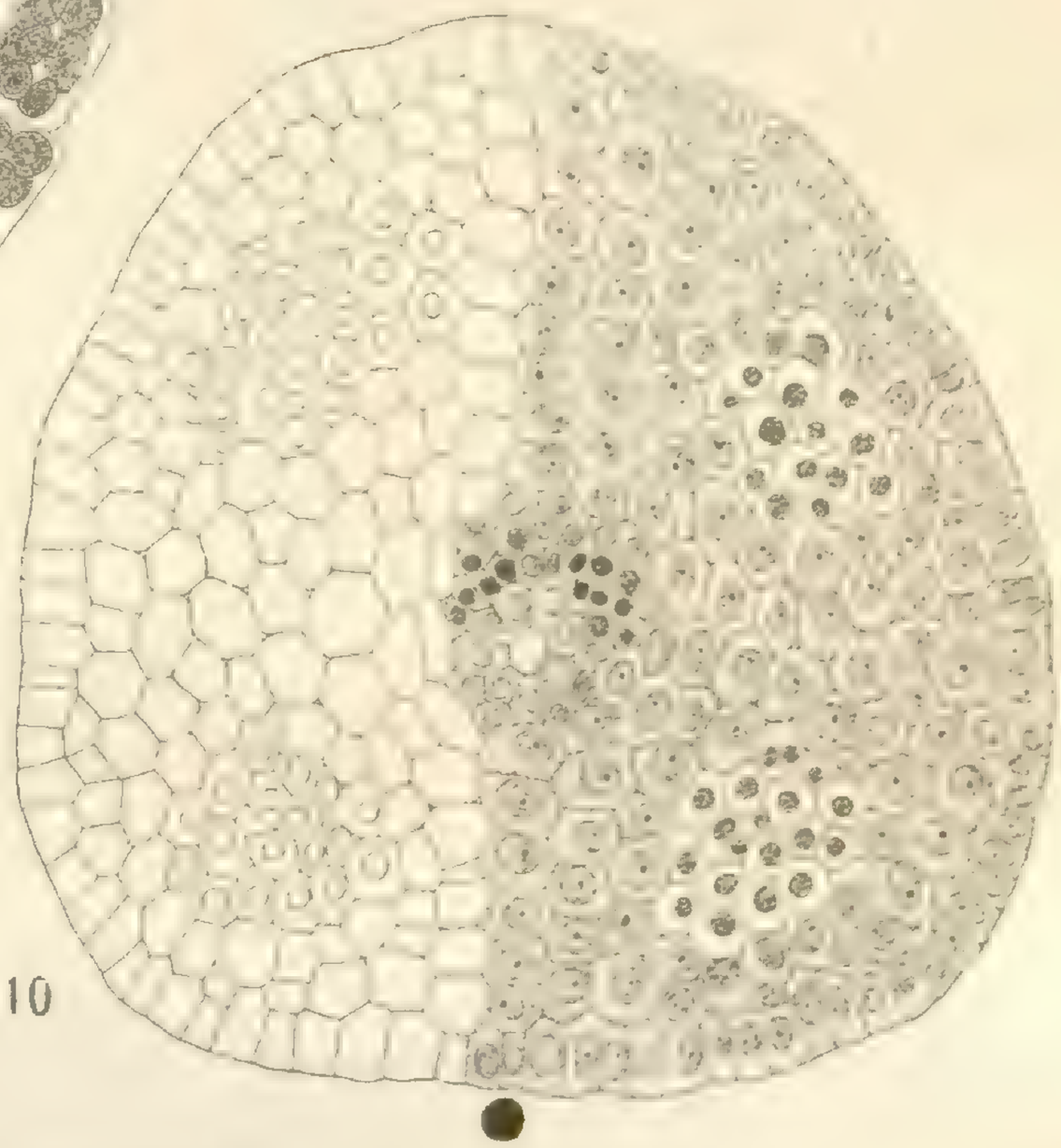

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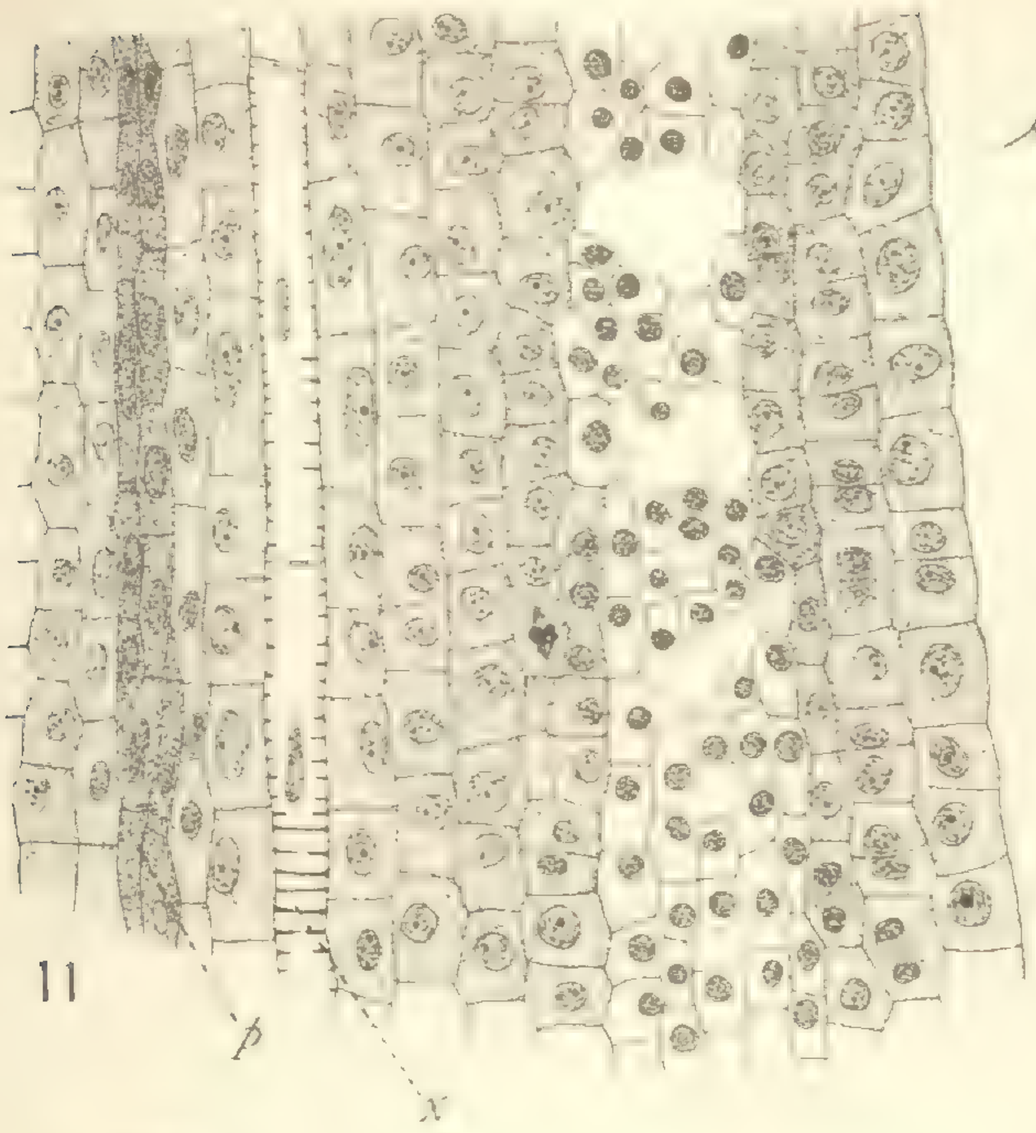

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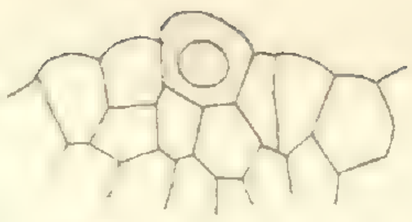

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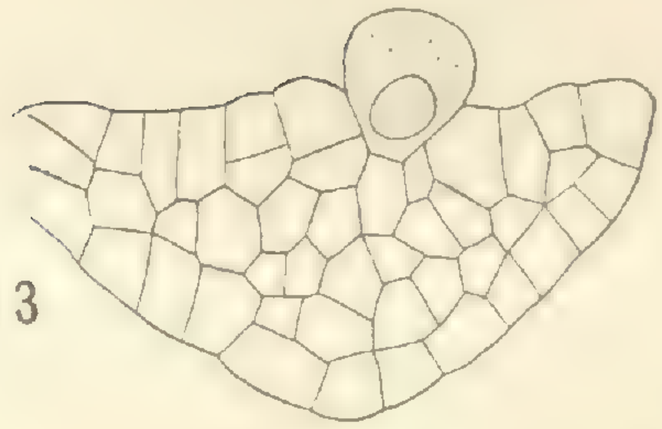

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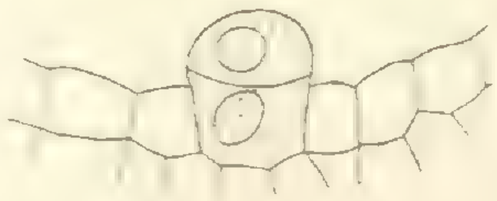

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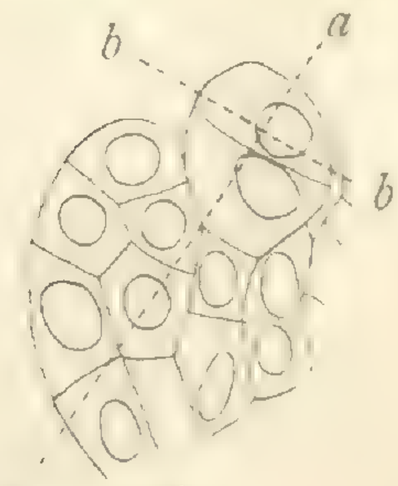

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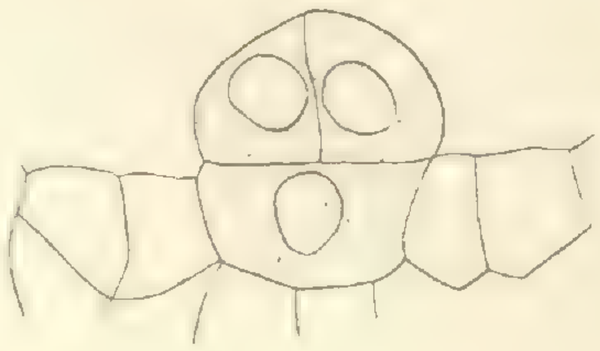

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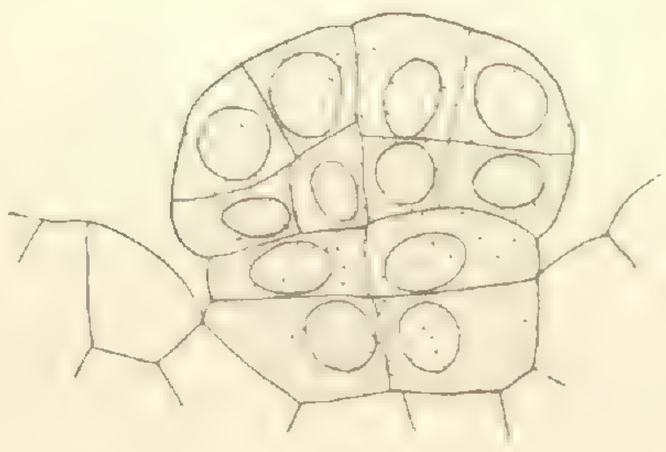

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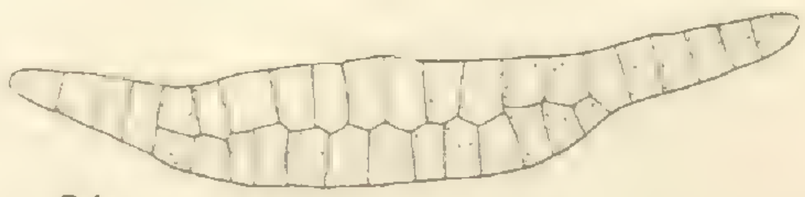

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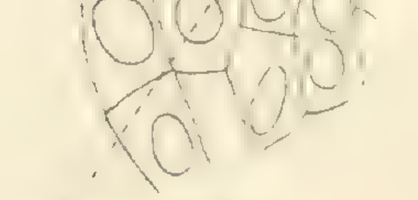

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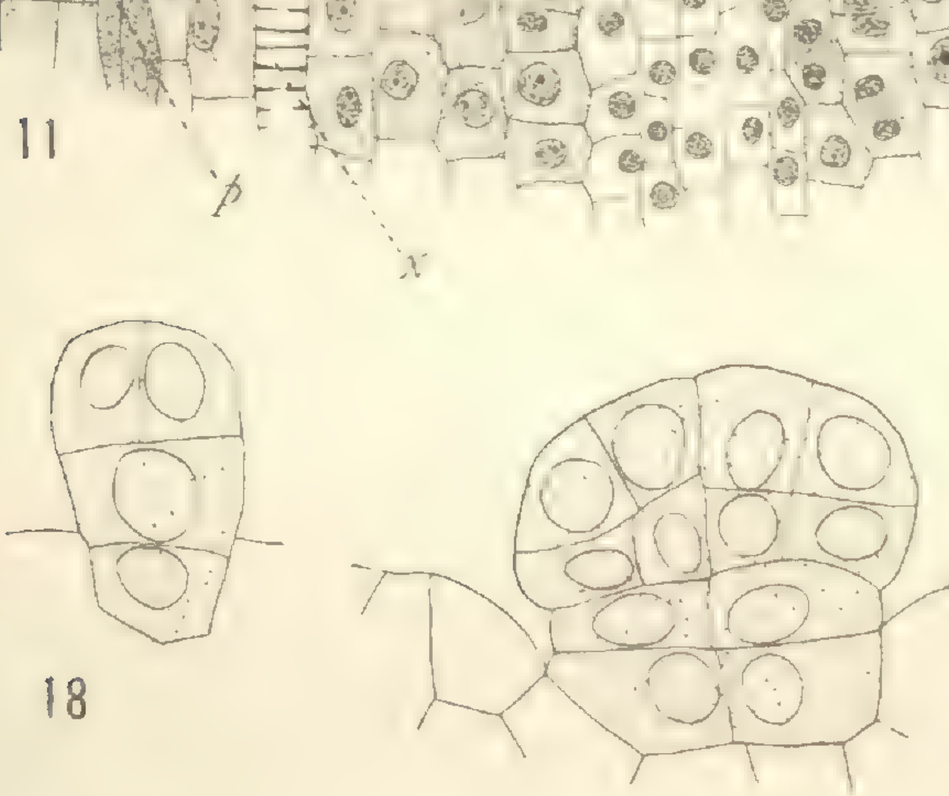

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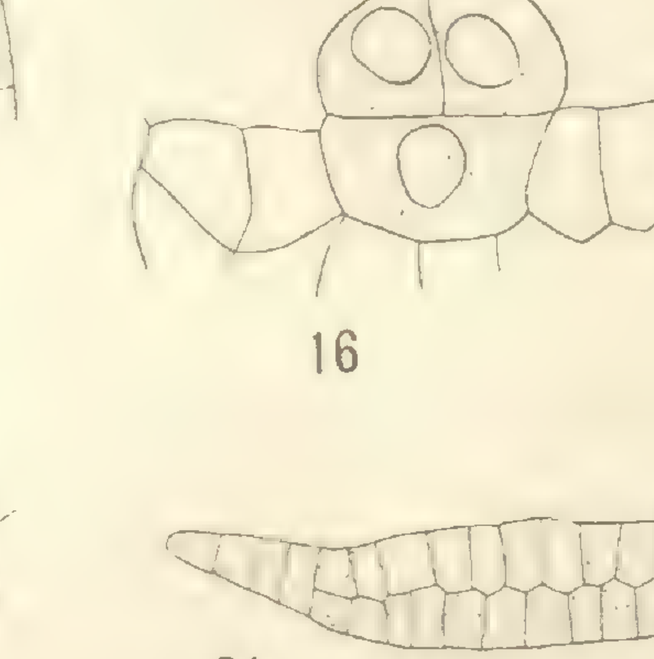

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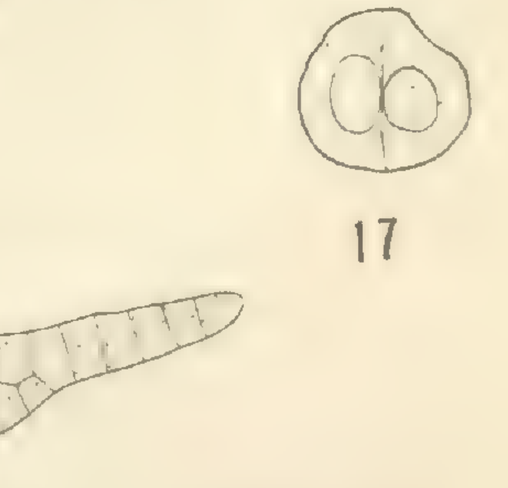

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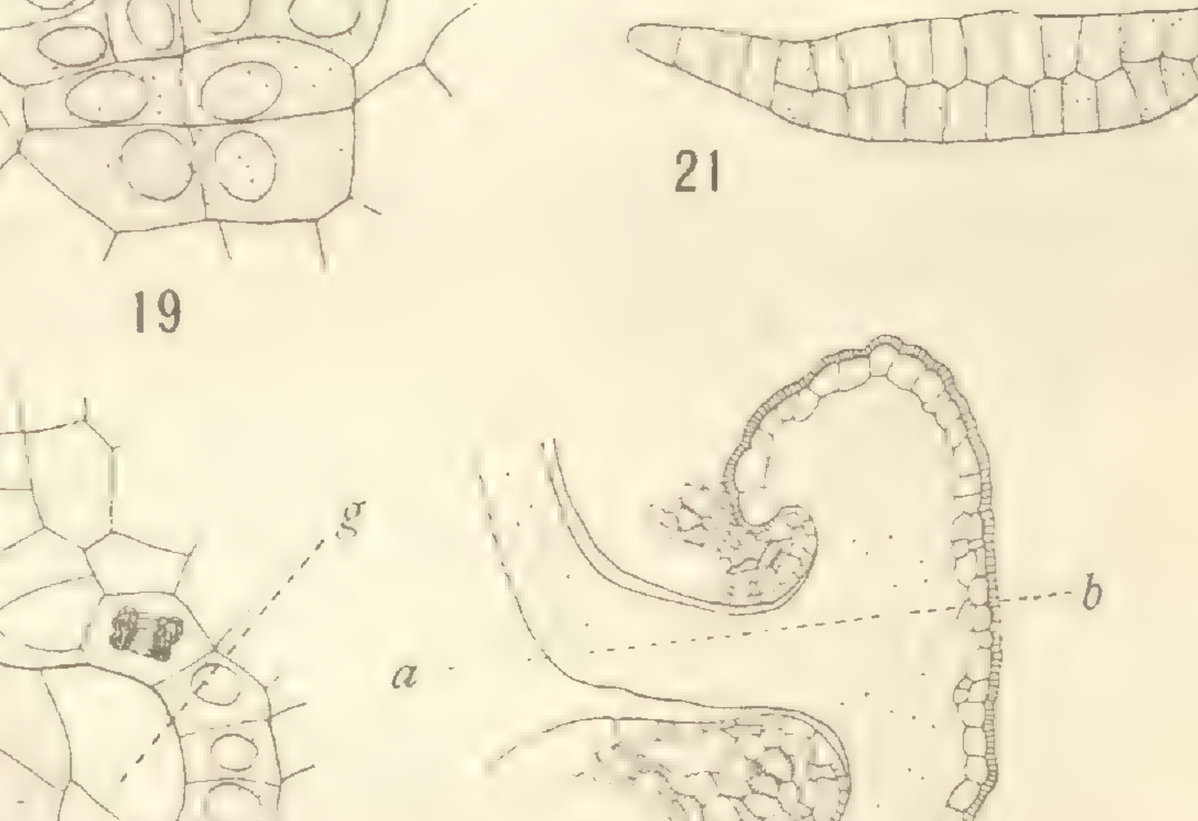

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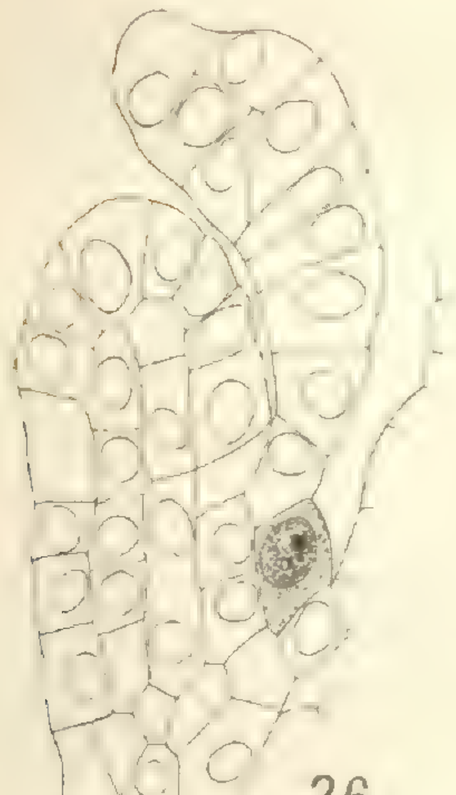

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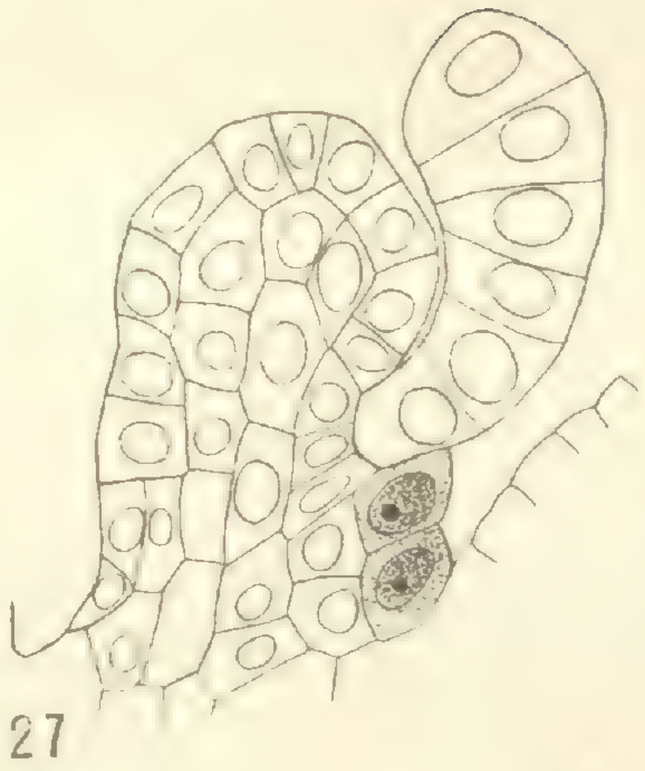

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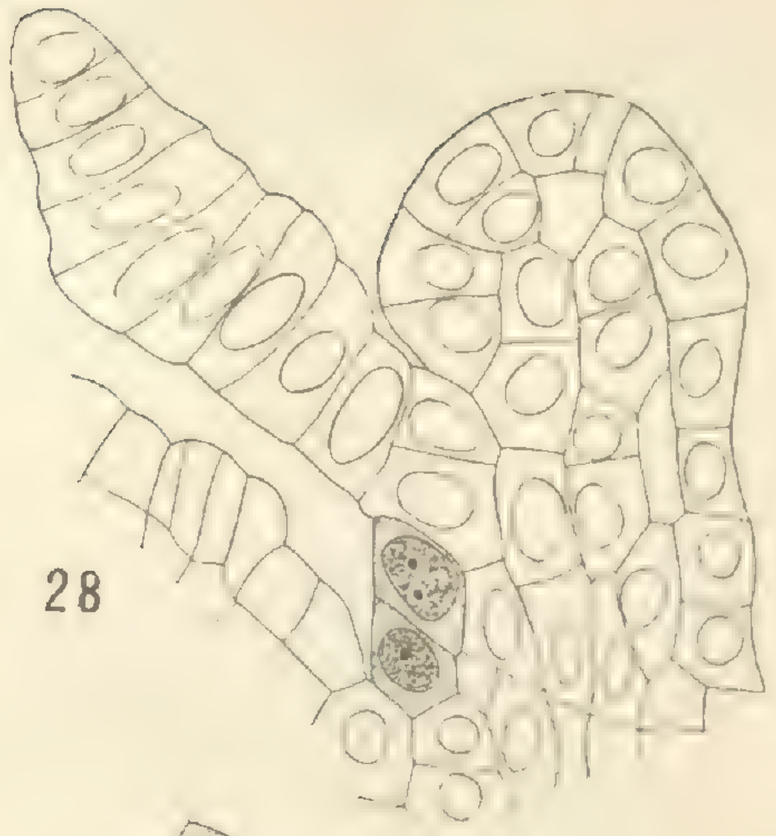

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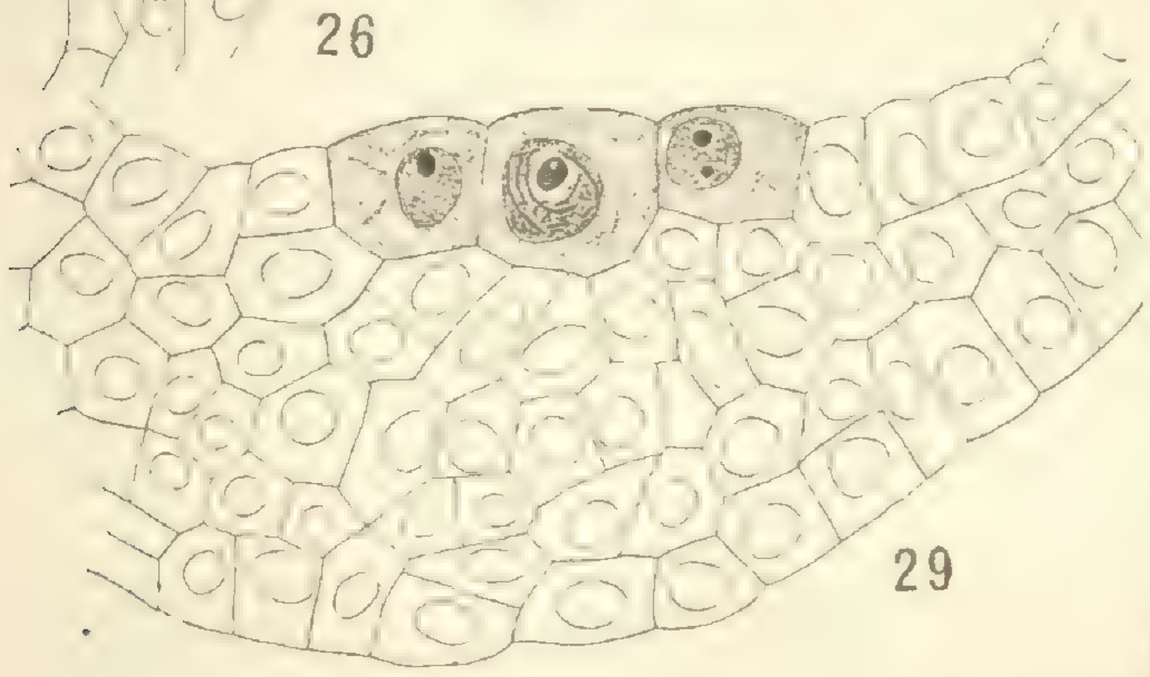

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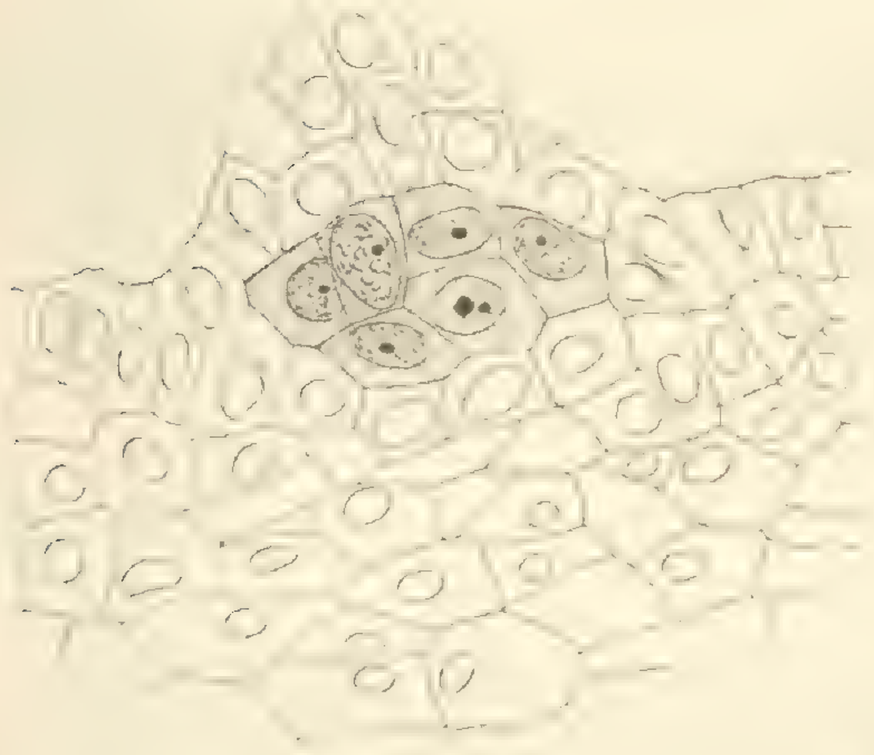

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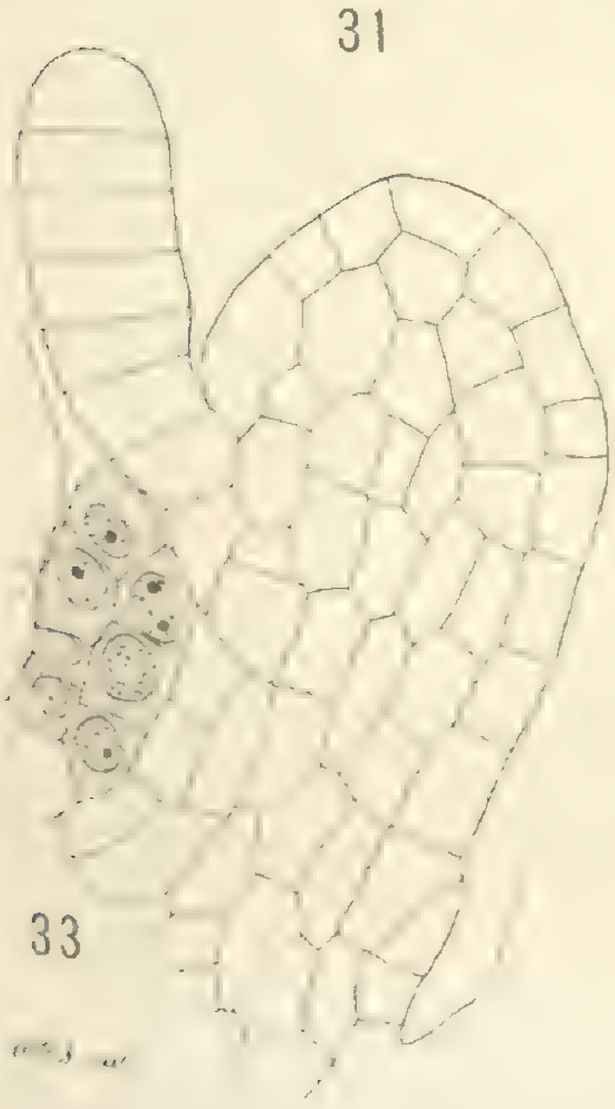

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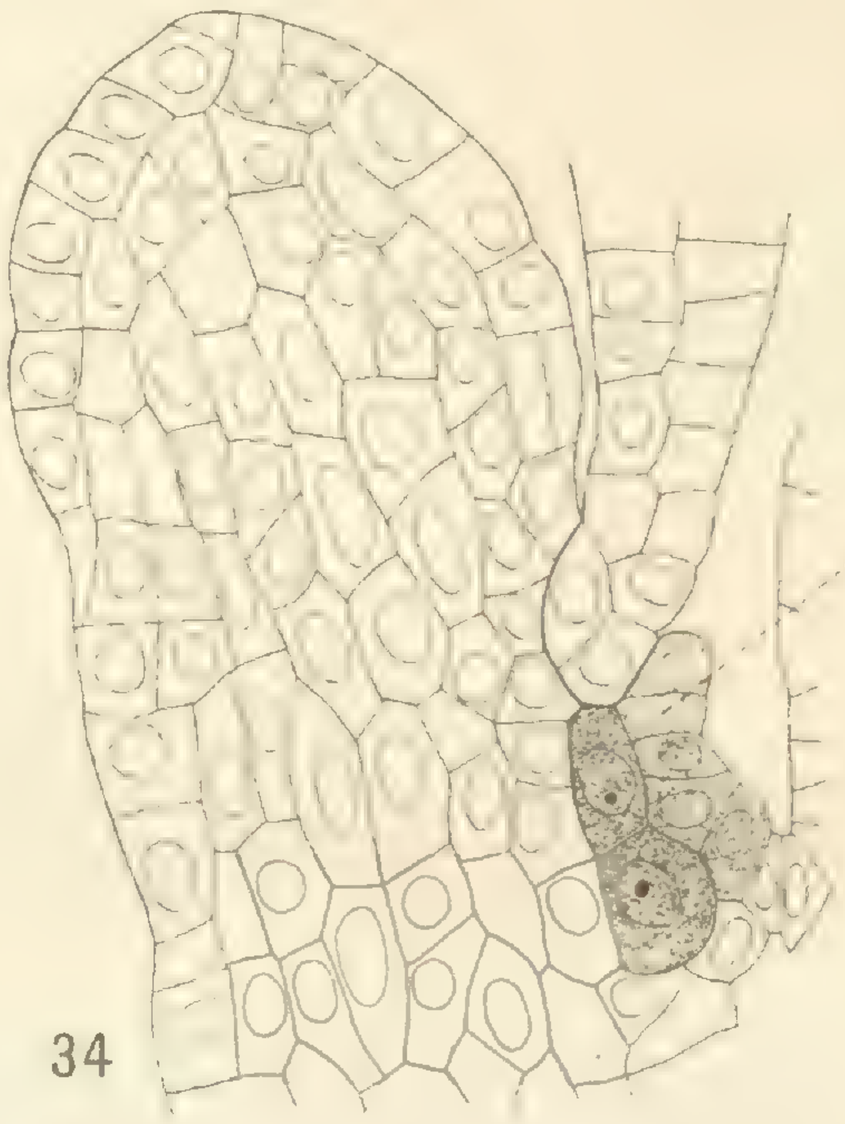

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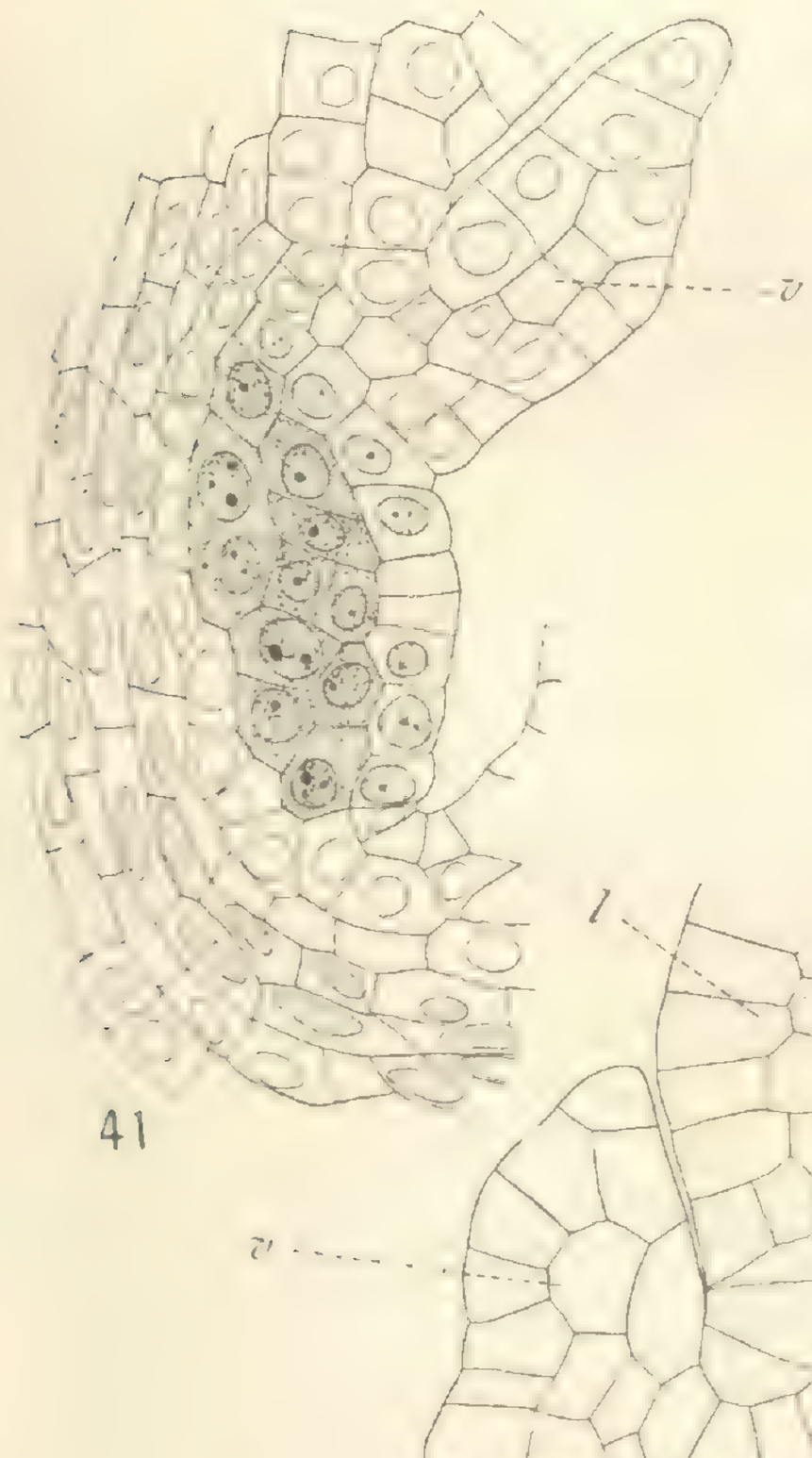

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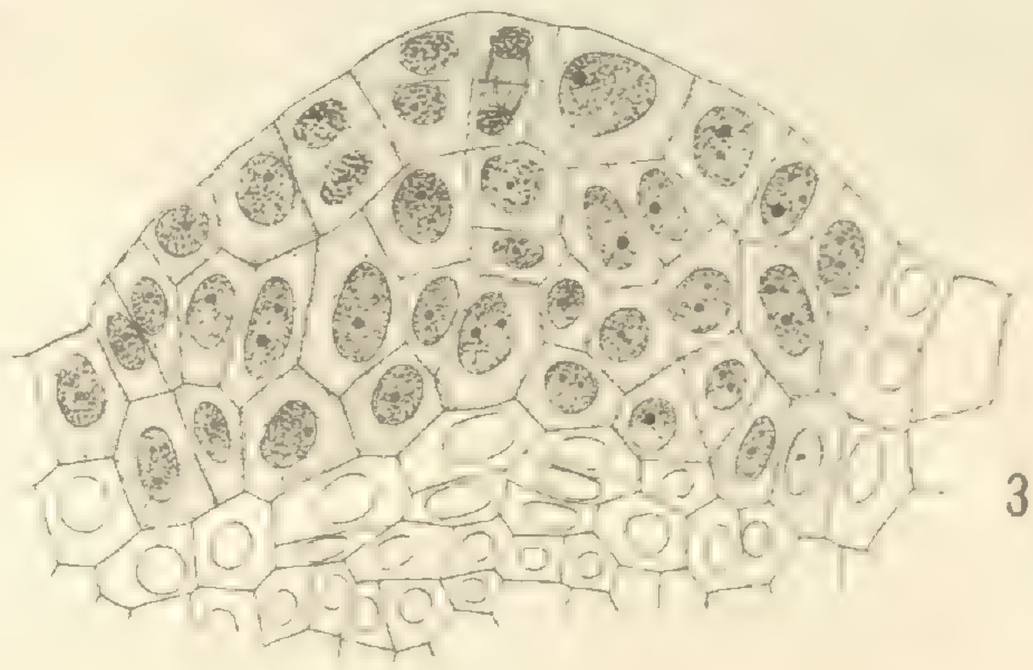

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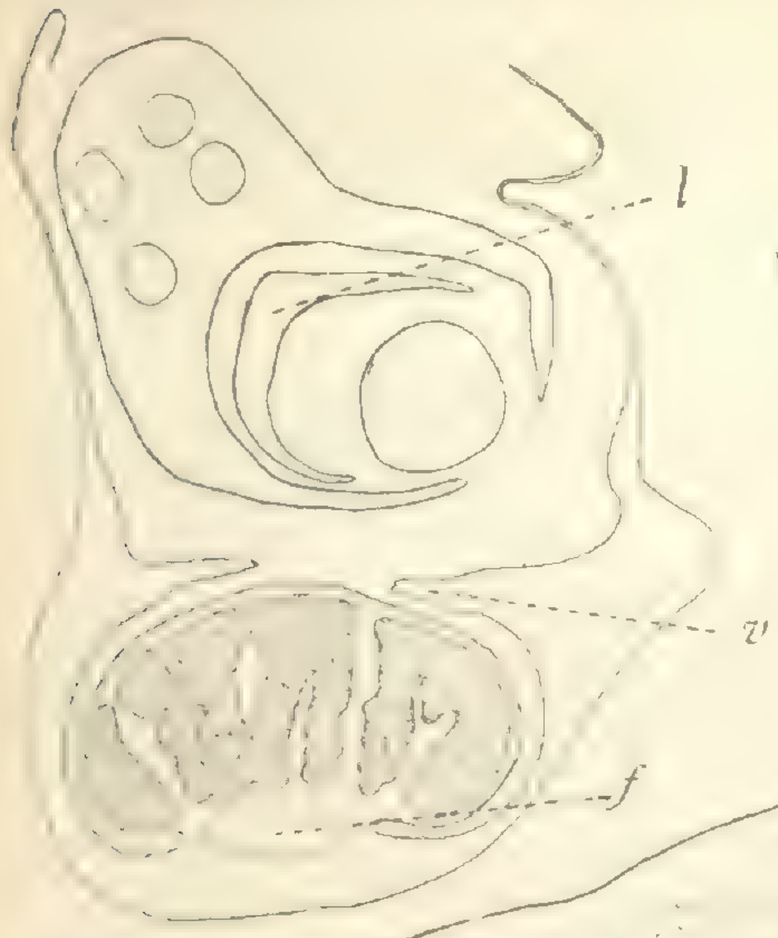

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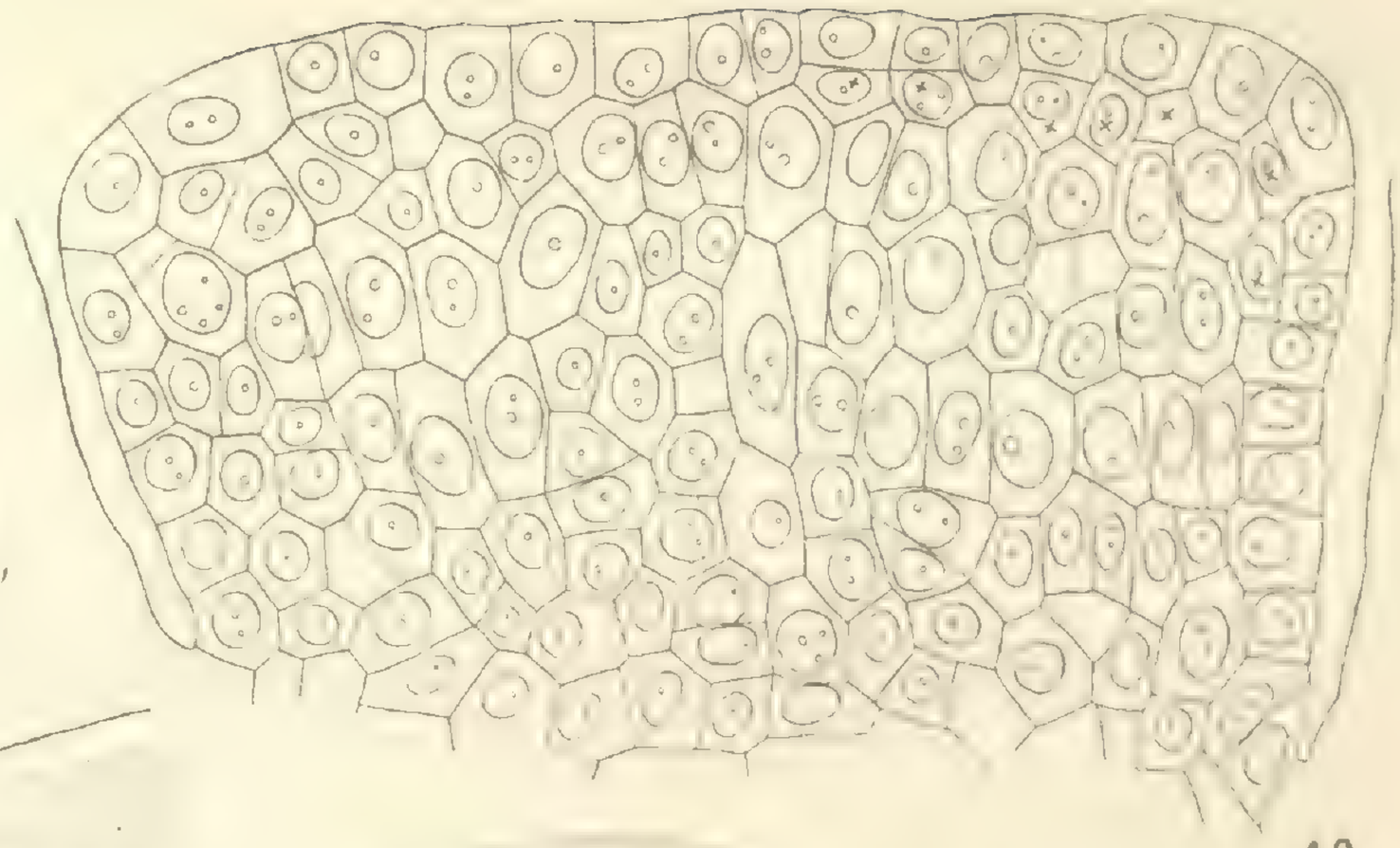

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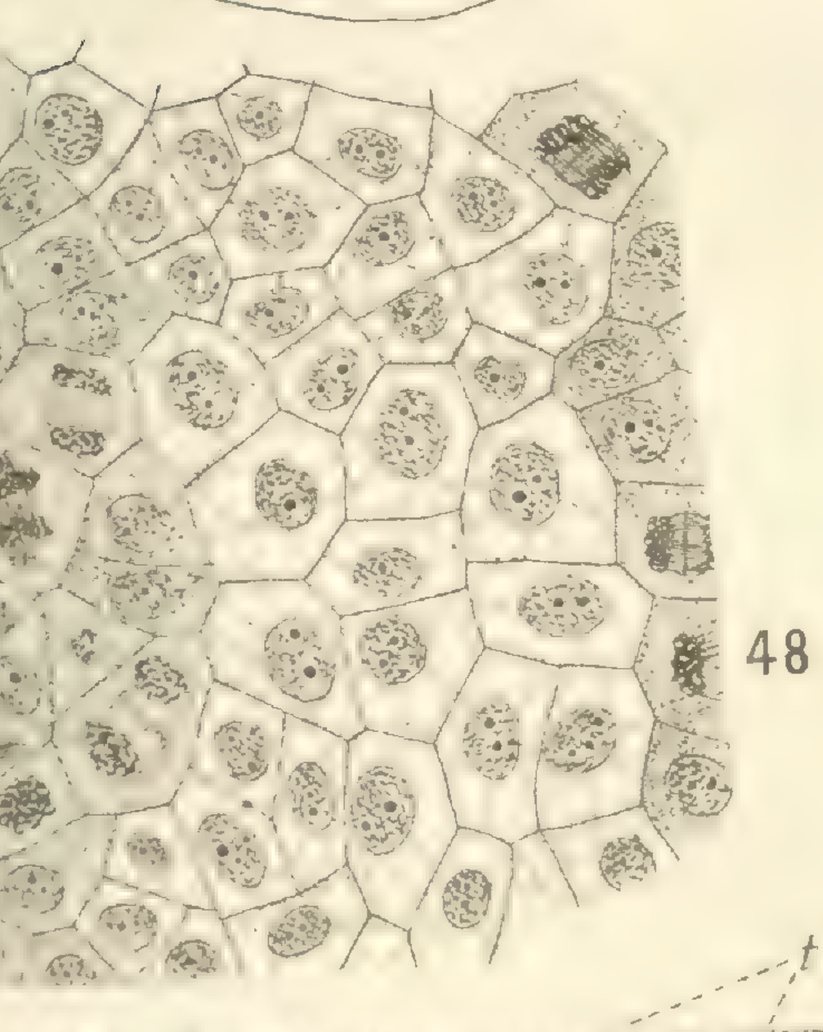

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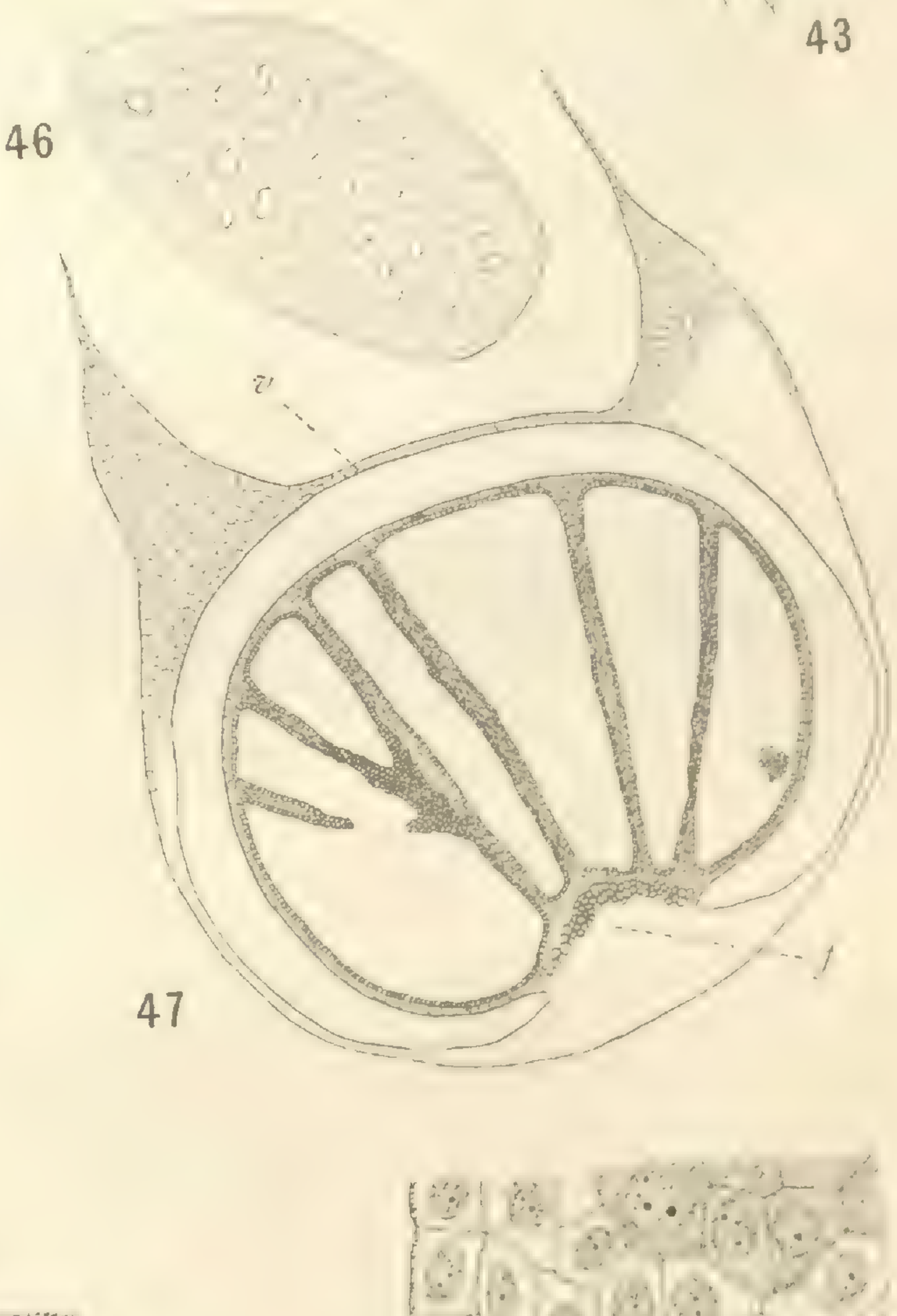

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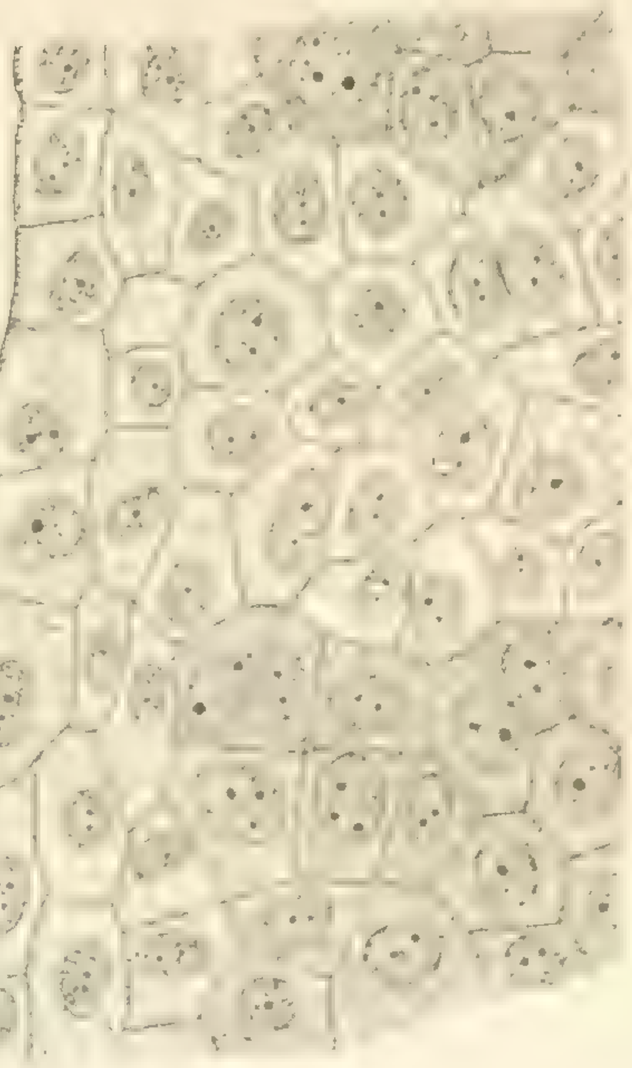

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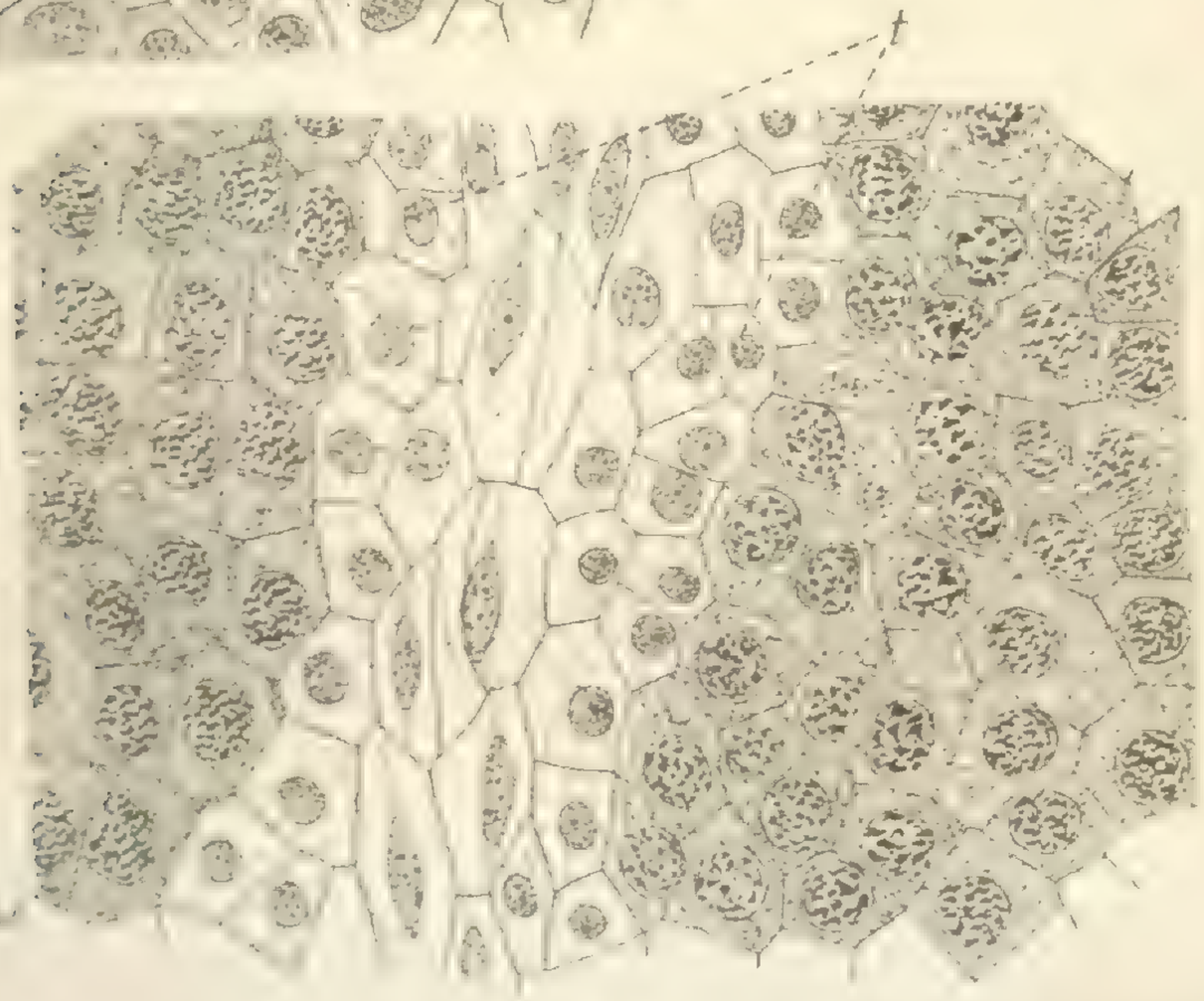

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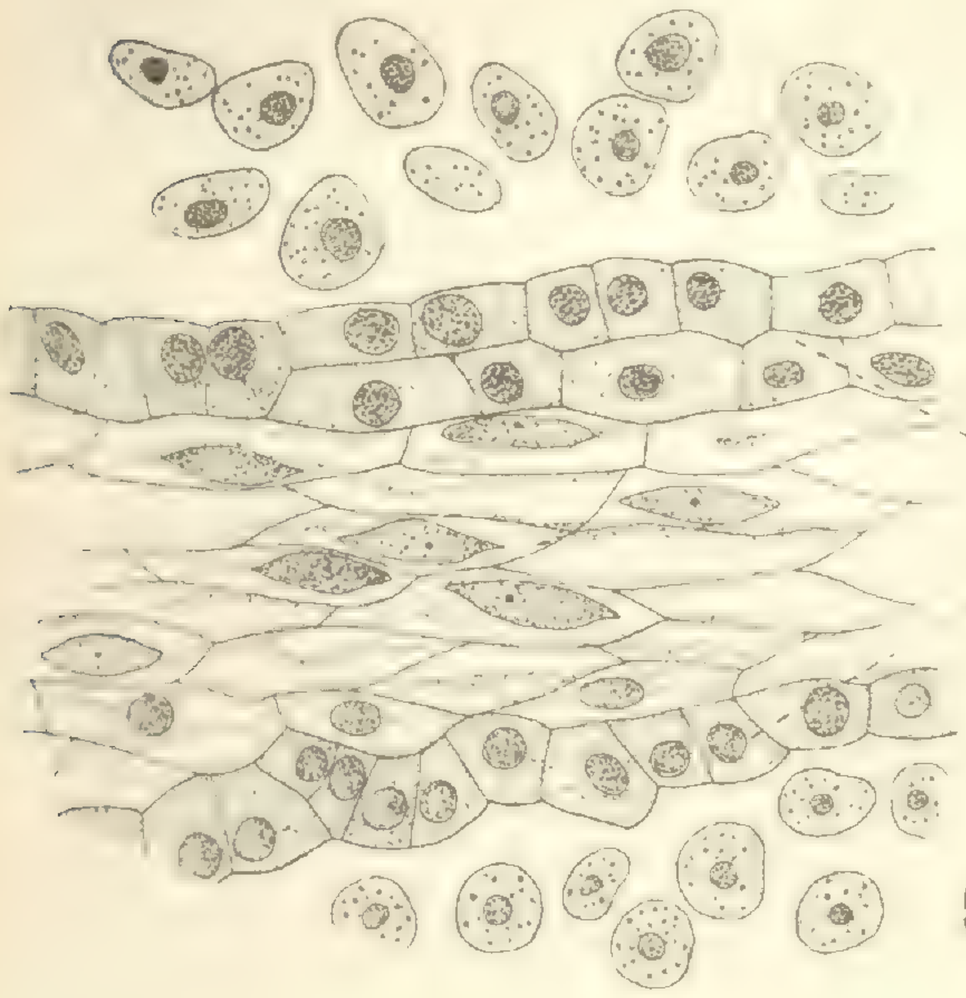

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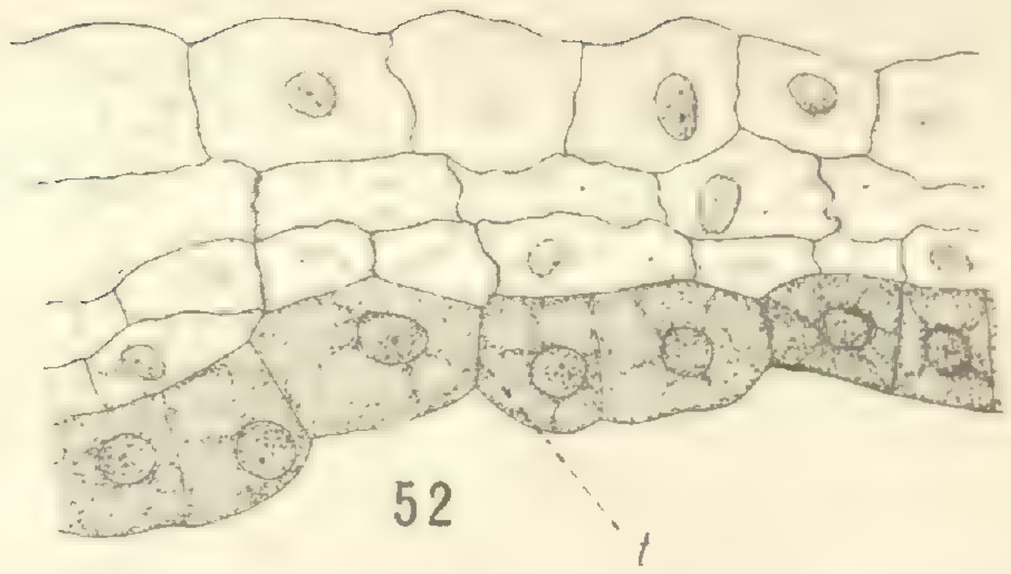

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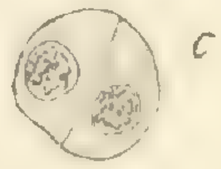

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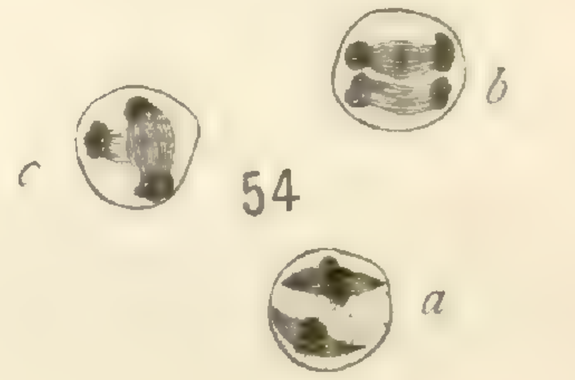

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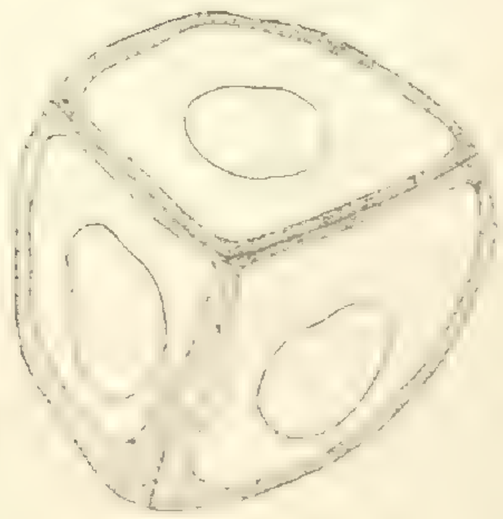

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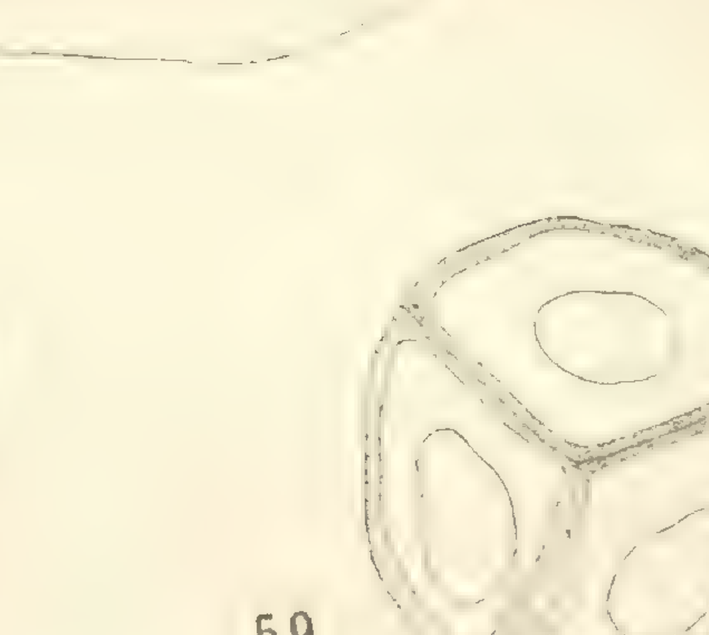

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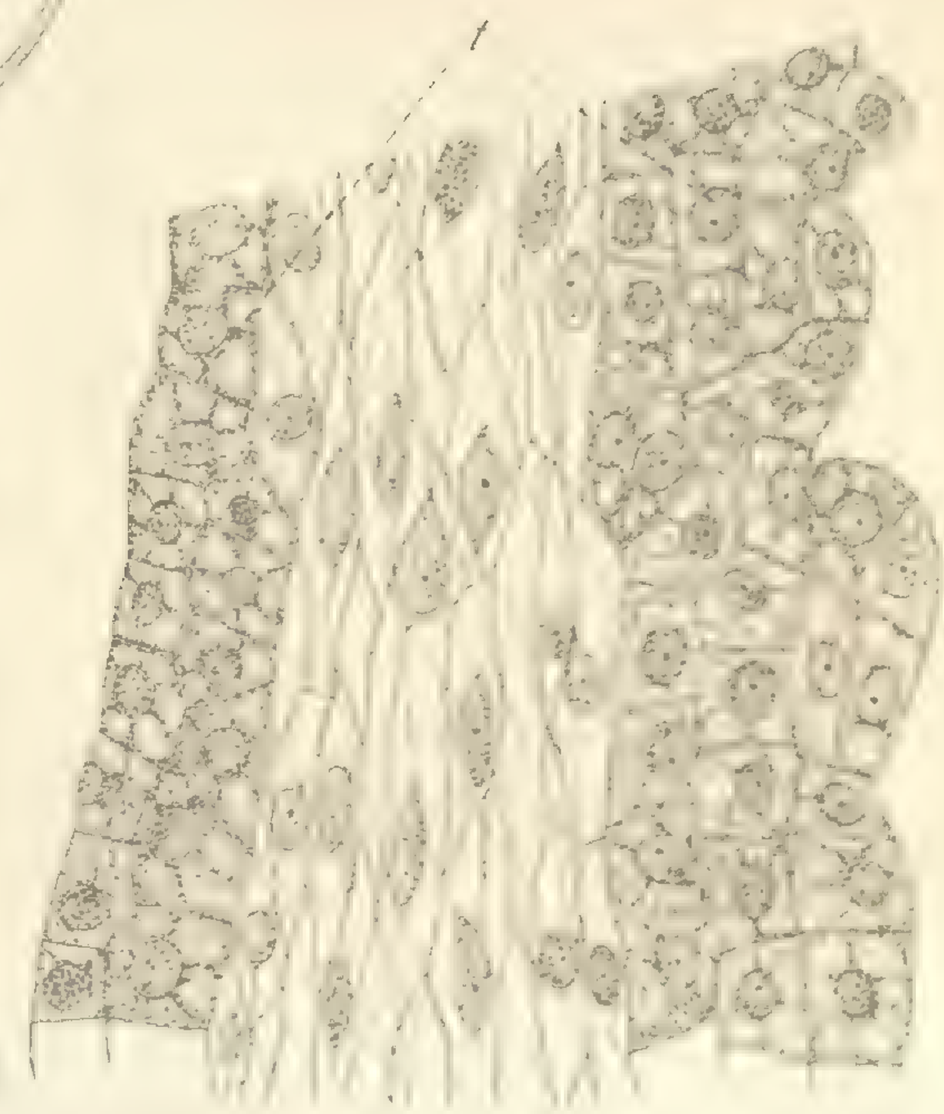

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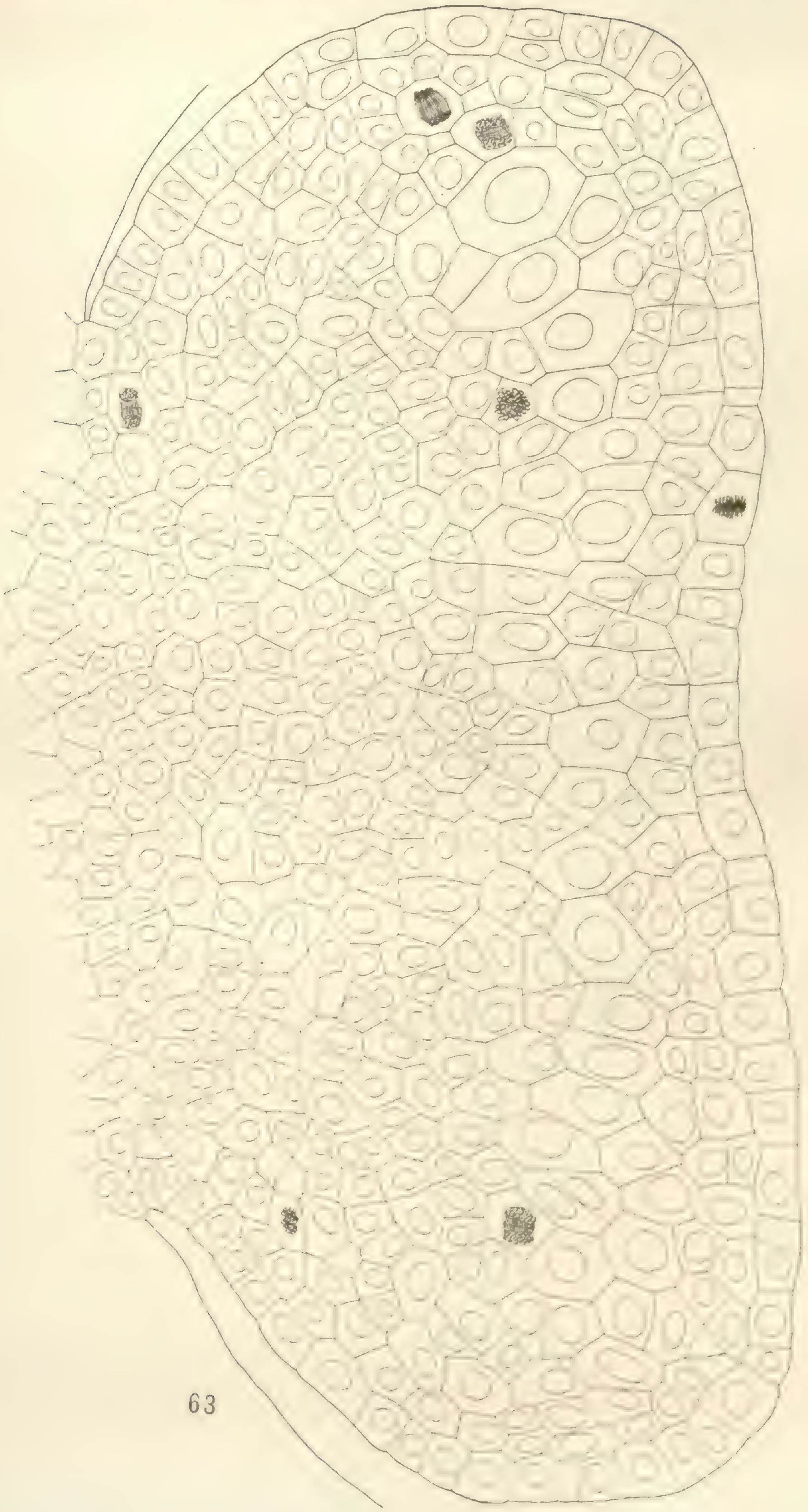

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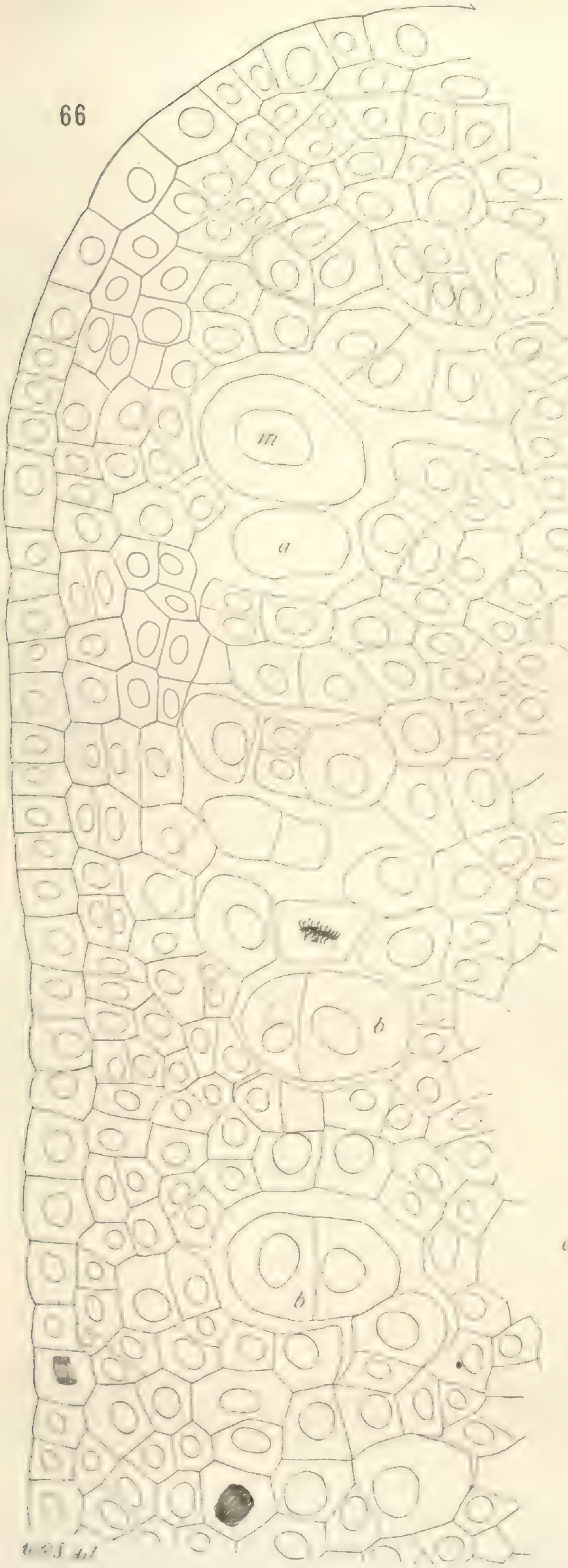

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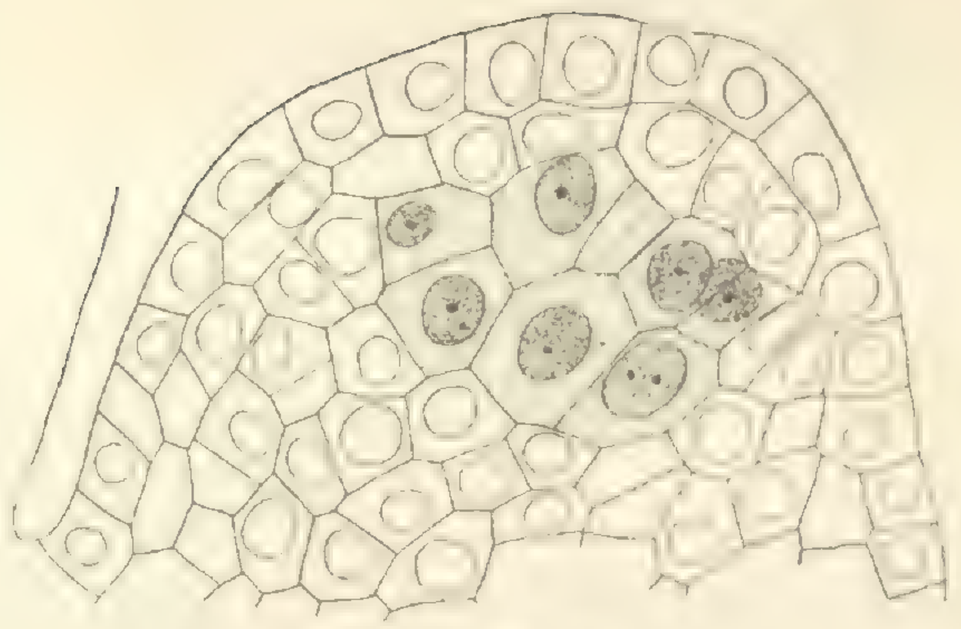

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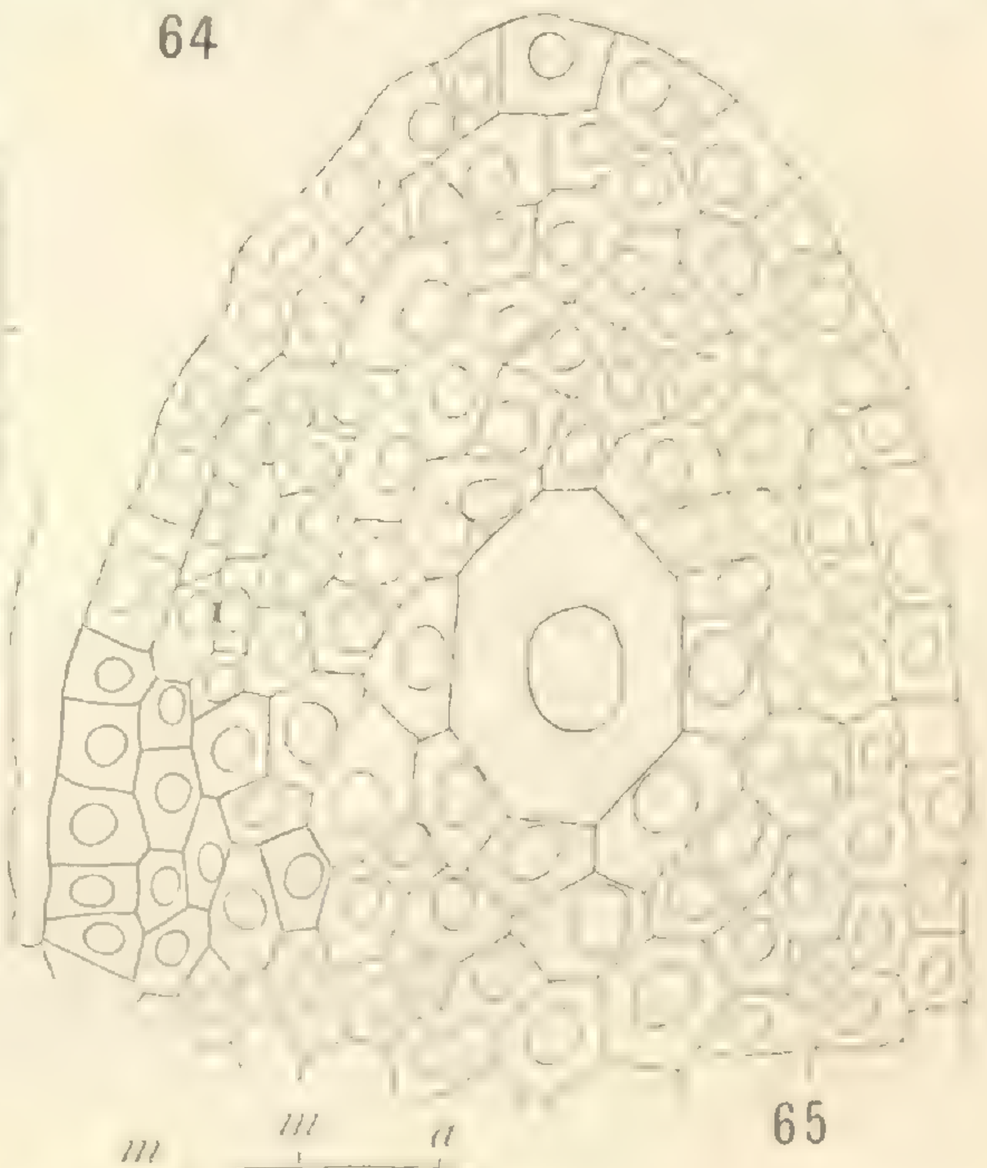

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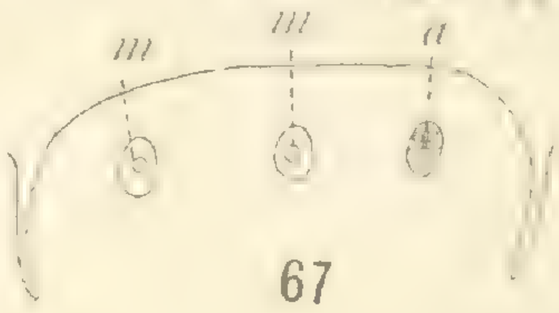

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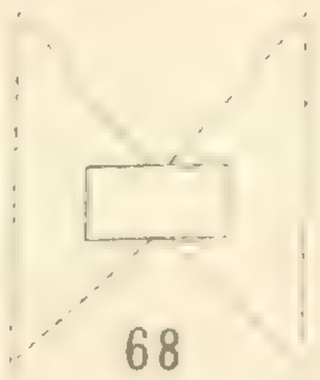

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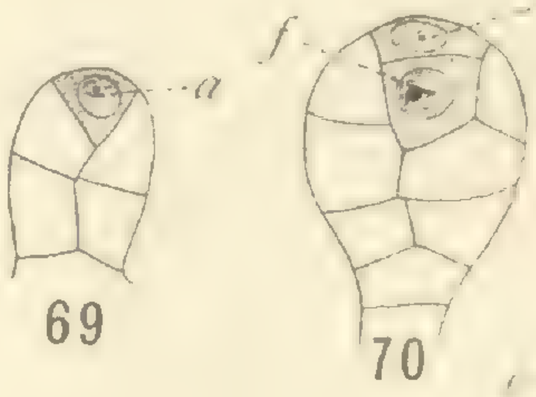

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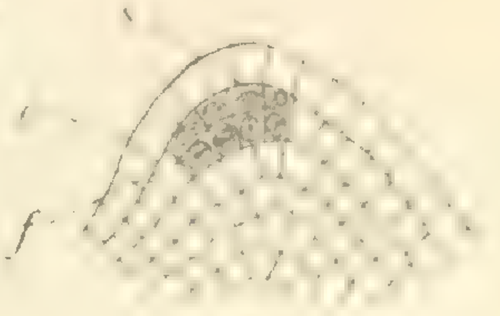

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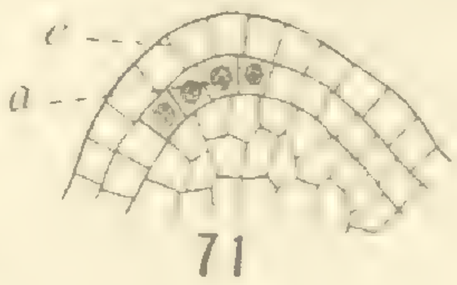

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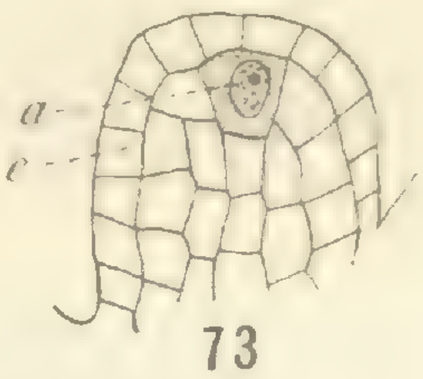

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CONTRIBUTION FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY. XLIII.

NOTE ON THE STRUCTURE AND REPRODUCTION OF COMPSOPOGON.[1]

ROLAND THAXTER.

(WITH PLATE XXI)

THE genus *Compsopogon* Mont., which is the sole representative of the Compsopogonaceæ, includes a few described species of filamentous algæ inhabiting the warmer regions of the earth, which are distinguished in general by their characteristic bluish or violet-green color, recalling that of some of the Myxophyceæ; while they are structurally peculiar from the fact that their filaments consist of an axial row of very large cells surrounded by one or more layers of corticating cells, the resultant structure closely resembling that of Ceramium among the Florideæ, though originating in a very different fashion.

The reproduction of these plants, although it has been very accurately interpreted by Schmitz (Engler & Prantl, Die nat. Pflanzenf., Algæ, p. 318) from an examination of dead material, has never so far as I am aware been directly observed, and since during a recent botanizing expedition in Florida I had an opportunity to study an abundance of fresh material, a special effort was made to obtain definite information on this point.

This alga was first met with at Cocoanut Grove in November 1897 along the shores of Biscayne Bay, growing most abundantly beside the road to Miami just north of the village, in ditches fed by bubbling springs which doubtless originating in the Everglades and traversing the narrow intervening strip of coral rock formation emerge in all directions along the bay and even mingle with the salt water at some distance from the shore.

[1] The substance of this Note was read at the New Haven meeting of the Society for Plant Morphology and Physiology, December 27, 1899.

The water along the margins of the bay is consequently in many places largely diluted in this way, so that, although the ditches above mentioned were repeatedly covered by the high tides during my stay, the water they contained was seldom perceptibly brackish.

A second locality was found at Daytona, a more northern station on the Halifax "river," where the alga occurs abundantly quite above and beyond any tidal influence in the rapidly flowing waters of the "canals," several of which intersect the town toward the south at right angles to the shores of the "river." A large mass was also found floating in a stagnant ditch on the Port Orange road south of Daytona, and it was seen to be conspicuously abundant in a brook which crosses the railroad just north of the New Smyrna station; while lastly a quantity was found on the margin of the St. John's river just below Jacksonville. In this connection it may be mentioned that specimens in the Herbarium at Harvard sent by Mrs. Curtiss are said to have been found in "tidal water" in the Hillsborough river near Tampa in west Florida; while it is further reported from Greencove and Blue Springs in the St. John's river region, as well as from Jupiter inlet on the east coast.

It is thus evident that Compsopogon is widely distributed and probably common in Florida; and that, although it may occur in tidal water that is practically fresh, it is characteristically an inhabitant of waters in which there is no admixture of salt.

Concerning the species of Compsopogon very little appears to be known and but few forms have been described; the brief list, exclusive of one or two uncertain species, comprising *C. leptoclados* Mont., from Guiana; *C. chalybeus* Kuetz., from Guiana, Porto Rico, and Florida; *C. aeruginosus* (J. Ag.) Kuetz., from Cuba; *C. coeruleus* (Balbis) Mont., from Florida, the Antilles, and Algeria; and *C. Corinaldi* (Menegh.) Kuetz., which has an apparently very limited distribution in Italy; to which, according to De Toni (*Sylloge* 4: 29), should be added *C. lividus* (Hooker) De Toni from Madras. That some of these are merely synonyms seems hardly doubtful, and so far as can be

determined by published figures and descriptions few of them appear to be distinguished by characters that might not be included in the variations of a single species.

In regard to the specific determination of the species which I examined in Florida it should be mentioned that the form occurring at and near Daytona has been kindly compared by M. Bornet with specimens of *C. coeruleus* from Porto Rico in Montagne's herbarium with which it seems to be beyond question identical. The Cocoanut Grove material, however, though it can hardly be separated by any distinctive microscopic characters, is macroscopically strikingly different when fresh, being paler greenish in color, soft and pliable to the touch, and much smaller: for though its filaments are rarely more than five or six inches long those of the Daytona material normally attain a length of two feet or more, their diameter being proportionately greater; while the whole plant has a characteristically harsh stiff feel and a deeper and more striking violet-blue-green color.

Whether these peculiarities should be attributed to a specific difference, or whether they merely represent variations of a single species due to a slight difference of environment resulting from the presence or absence of tidal influence, for example, is uncertain. In either case the younger filaments and their branches consist of single rows of rather flattish cells with numerous oval to oblong or nearly spherical chloroplasts, some of which lie immediately about the conspicuous nucleus; while the greater part are peripherally disposed, being held in a protoplasmic reticulum (*fig.* 1), the active circulation in which is very conspicuous. These chloroplasts, which often exhibit a slow change of position in the protoplasmic mesh, vary but slightly in shape, and in no instance were any elongate or thread-like forms seen like those described and figured by Schmitz (*l. c.*) as characteristic of *C. coeruleus*. The filaments increase in length through intercalary divisions, and at no great distance from the terminal cell longitudinal septa begin to make their appearance, irregularly at first, but succeeding one another in such a fashion that a central axial cell comes to be separated from a layer of peripheral

cells that completely surround it and continue to undergo anticlinal divisions without regularity, while the axial cell constantly enlarges, assuming a flattened barrel-shaped form. The originally single cells of the younger filaments are thus converted into corticated segments indicated by slight constrictions in the older filaments; the monstrously developed axial cells, which are filled with watery contents and contain few chloroplasts, forming a continuous series (*fig. 14*). The corticating cells which are irregularly polygonal (*fig. 7*) form, according to Schmitz, but a single layer even in the oldest filaments; but although this seems to be invariably the case in the material from Cocoanut Grove, as shown in the figure last cited, it by no means applies to the Daytona form in which, although the original axial cells appear to remain undivided, periclinal divisions take place by which the corticating cells are separated into two well-defined layers (*fig. 12*), as is also indicated in Kuetzing's *Tabulae Phycologicae* 7: *pl. 88, figs. b* and *f*, which may be increased to three or even four in older axes like that shown in *fig. 13*, a portion of the axial cell being indicated at *x*.

The filaments of Compsopogon are always more or less copiously branched, and although short secondary branches are sometimes developed from the corticating cells, the primary ones appear in all cases to be formed by the direct outgrowth of one of the undivided cells of the younger filaments. The alga when growing in still water may remain unattached, but is usually fixed to sticks, stones, or other plants, a short series of cells at the base remaining uncorticated and sending down rhizoidal outgrowths which form an attachment analogous to that of Porphyra.

An examination of the Cocoanut Grove material showed further that, although the cells of a majority of the plants gave no indication of any differentiation that might suggest a preparation for some form of reproduction, in others the cells of the cortex as well as those of the younger uncorticated branches had evidently divided in a characteristic fashion; one, usually the smaller of the two resultant cells, being conspicuously differentiated by reason of its darker color and more dense contents;

but although these cells were kept under observation for several hours during the afternoon and evening of the day on which they were collected no separation of spores was noticed. On the following morning, however, the dark cells were found to have disappeared, while the filaments presented the normal appearance. Although no empty cells were visible from which spores might have escaped, it was evident that something of this nature had occurred during the night. A second attempt was therefore made on the following evening; but nothing having transpired, a filament, in which many hundreds of these dark cells were present, was placed in a Van Tieghem cell shortly after nine o'clock and left till morning, when it was found to have resumed its normal appearance as before. In place of the dark cells, however, which had disappeared, a corresponding number of spherical green free cells were found lying motionless in the water at a short and rather constant distance from the filament, having evidently escaped during the night. Observations were therefore resumed at a later hour on the following evening, and at about eleven o'clock I was rewarded by seeing the first aplanospore make its escape. The same type of reproduction was repeatedly observed on subsequent occasions, and may be summarized as follows:

Formation of macroaplanospores.— Any of the superficial corticating cells, even in the oldest portions of the plant, or any of the cells of the younger filaments, even before the divisions preceding cortication have taken place, may become separated during the night into two daughter cells, in one of which the contents is more dense than in the other, and the nucleus larger and more conspicuous. As the day advances the oval chloroplasts by repeated division eventually fill it almost completely, and it begins to assume a sub-triangular outline; one of the rounded angles projecting in the form of a papilla, the wall of which is more or less distinctly thickened, the contents just beneath it becoming nearly or quite free from chloroplasts (*fig.* 1). As this cell or monosporangium matures, the basal septum by which it was originally separated from the other

daughter cell bulges more and more strongly towards the latter, and finally the discharge of the spore is accomplished, as in other instances where a papilla for dehiscence is formed, slowly at first and then more rapidly; while during its discharge, the basal septum reverses its position, the pressure exerted by the contents of the adjacent cell pushing it back into the monosporangium as the latter empties (*figs. 2–4*), the process continuing after the spore has escaped until the cavity is wholly obliterated, so that in a few hours the position of the sporangium is merely indicated by the slightly projecting margins of the orifice through which the spore escaped.

The spore, which is discharged with a force only sufficient to carry it a very short distance from the filament, is quite spherical, completely filled with chloroplasts, except for a small area (*fig. 5*) which is free from them, and possesses not even a slight amoeboid motion. In the Van Tieghem cell a few of the spores became disorganized in a short time, while a great majority, secreting a distinct wall, began to germinate on the day following their discharge; and the young plants thus formed continued to grow, forming branching filaments, for more than a week, when the culture had to be abandoned.

This type of reproduction, which was frequently met with in the material examined at Cocoanut Grove as well as at Daytona, was very uniform in all cases, but just as I was preparing to leave the former locality, a tuft of small plants was found growing on submerged grass culms in water more than usually subject to tidal influence, among which forms having the normal type of sporulation were associated with others in which it was somewhat different. Although the peculiar characteristics of this second type of sporulation may be the result of unfavorable conditions and without special significance, it may be convenient on account of their small size to distinguish the spores formed in connection with it as microaplanospores.

Formation of microaplanospores.—The formation of the cells destined to produce microaplanospores resembles the first steps in the formation of the macroaplanosporangia in that any cells

of the cortex or of the younger uncorticated portions of the filaments may divide to form two cells, one of which is usually, however, far smaller than the other and often separated from it (*fig. 10*) by an oblique septum. These small cells, instead of being converted directly into sporangia, become pushed outward so as to occupy a more or less peripheral position, and soon begin to divide independently, at first by anticlinal septa only, the early divisions sometimes following one another at right angles with such regularity that the resultant cells may be in many cases so conspicuously arranged in groups of four as to suggest aggregations of tetraspores; a resemblance, however, which soon disappears, since the divisions follow one another with increasing irregularity, and may even become periclinal. The filaments thus become covered with scattered sori (*figs. 8, 11*) irregular in form as well as in the number of cells which compose them, and might well be mistaken for groups of parasitic algæ having a habit somewhat resembling that of Xenococcus.

The discharge of spores from the cells composing these sori was not actually observed, but preparations left over night in Van Tieghem cells showed that such a discharge undoubtedly takes place, the sori being surrounded by numerous aplanospores, which, like those of the normal type, were spherical and from their regular position evidently non-motile; but were, on the other hand, far smaller (*fig. 9*) and paler from the presence of a relatively much smaller number of chloroplasts. That these microaplanospores are similar in nature to the normal spores, and that they germinate directly is altogether probable; but the exigencies of my departure made it impossible for me to determine this as well as other points in connection with them. The appearance of the older sori suggests the conditions that have been figured in connection with the supposed formation of antherozoids in Bangia; but there was no indication that the bodies thus separated in Compsopogon were sexual in function.

A careful examination of the coloring matter of these plants would be a matter of no little interest, and it may be worthy of

mention that it is so readily soluble that the bowl of water used for mounting some of the dark colored Daytona material was soon tinged a deep, somewhat violet-blue, suggesting a slight mixture of phycoerythrin with phycocyanin.

The facts above presented, although they furnish definite information concerning the reproduction of this peculiar group, are not such as to make the true position of its members less obscure than they have been heretofore, since in general they substantiate the conclusions reached by Schmitz, based, as has been previously mentioned, on the examination of dead material. As this author has pointed out, their resemblance to forms like Ceramium in the gross structure of the thallus is wholly superficial, the cortications originating very differently in the two cases, and it seems quite certain that their near relatives are not to be sought among the higher Rhodophyceæ. It cannot be denied, however, that, so far as they are known, their reproductive processes are more directly comparable with those of the Bangiaceæ than of any other group, the aplanospores of Erythrotrichia being similar to those of Compsopogon and similarly produced. That the paler "microaplanospores" of the latter genus may correspond to the "antherozoids" of the Bangiaceæ is not impossible, and although no indication of any sexual process was observed in the material examined, it may occur under other conditions or at other seasons of the year. Admitting, however, that these bodies are probably not sexual in nature, it may be remarked that the same might be said of bodies to which this function has been attributed among the Bangiaceæ; so that in either case it would seem more in accordance with the ascertained facts to leave the family in question among the doubtful Bangiales, in the absence of any other group to which they seem as closely related. Yet, although this is the position actually assigned to them by Schmitz (*l. c.*), he finally remarks, "Am besten dürfte es sein die Compsopogonaceæ als eine etwas isoliert stehende Grüppe vegetativ hoch entwickelter Formen den grünen Algen zuzuzählen."

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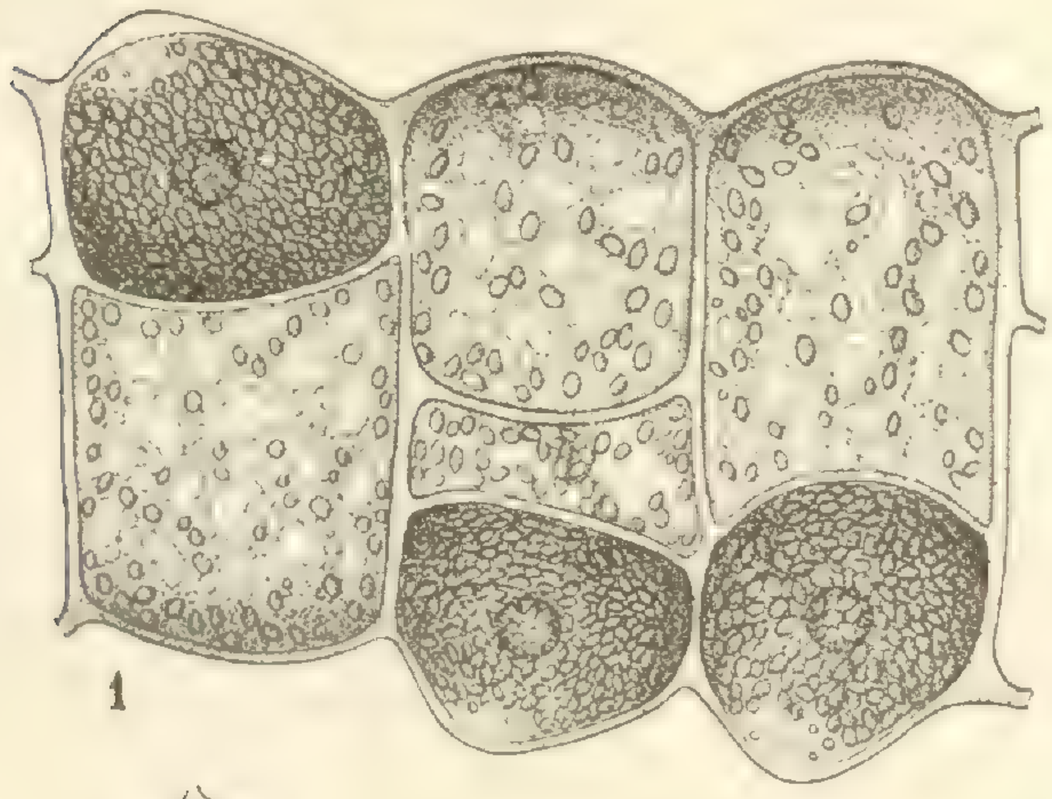
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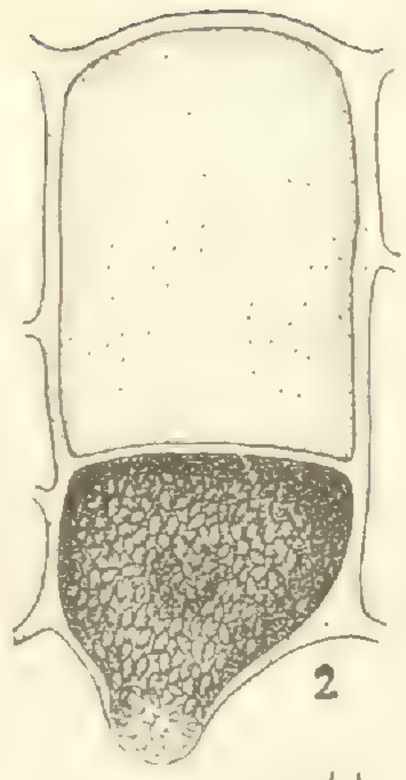
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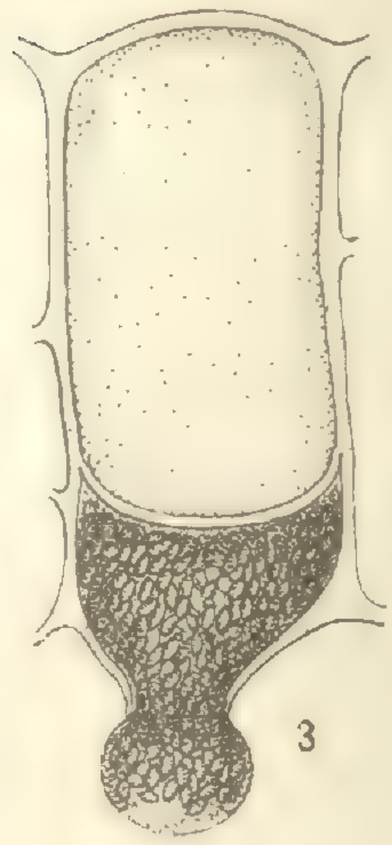
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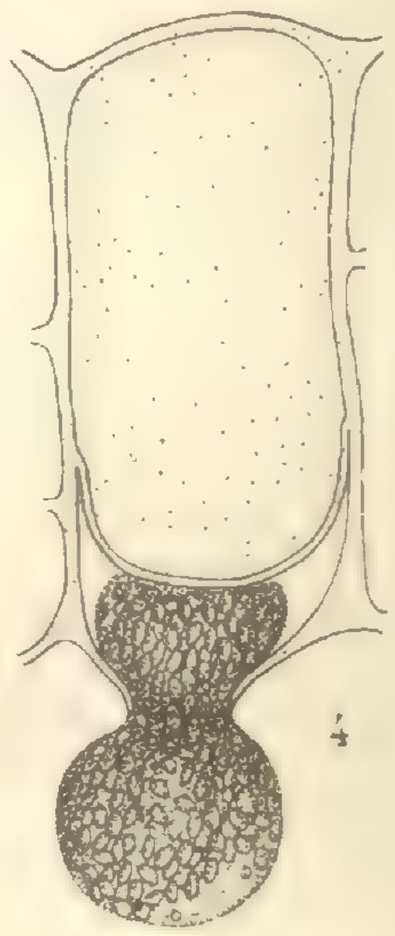
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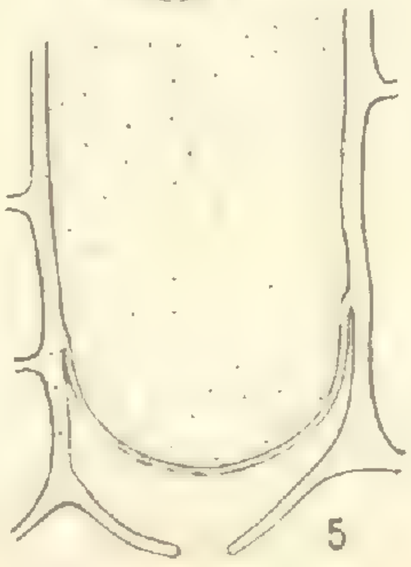
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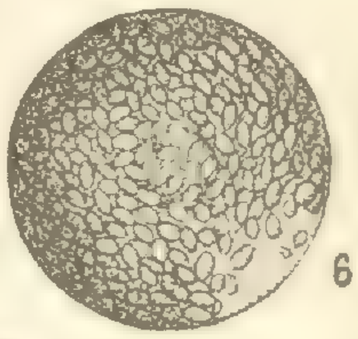
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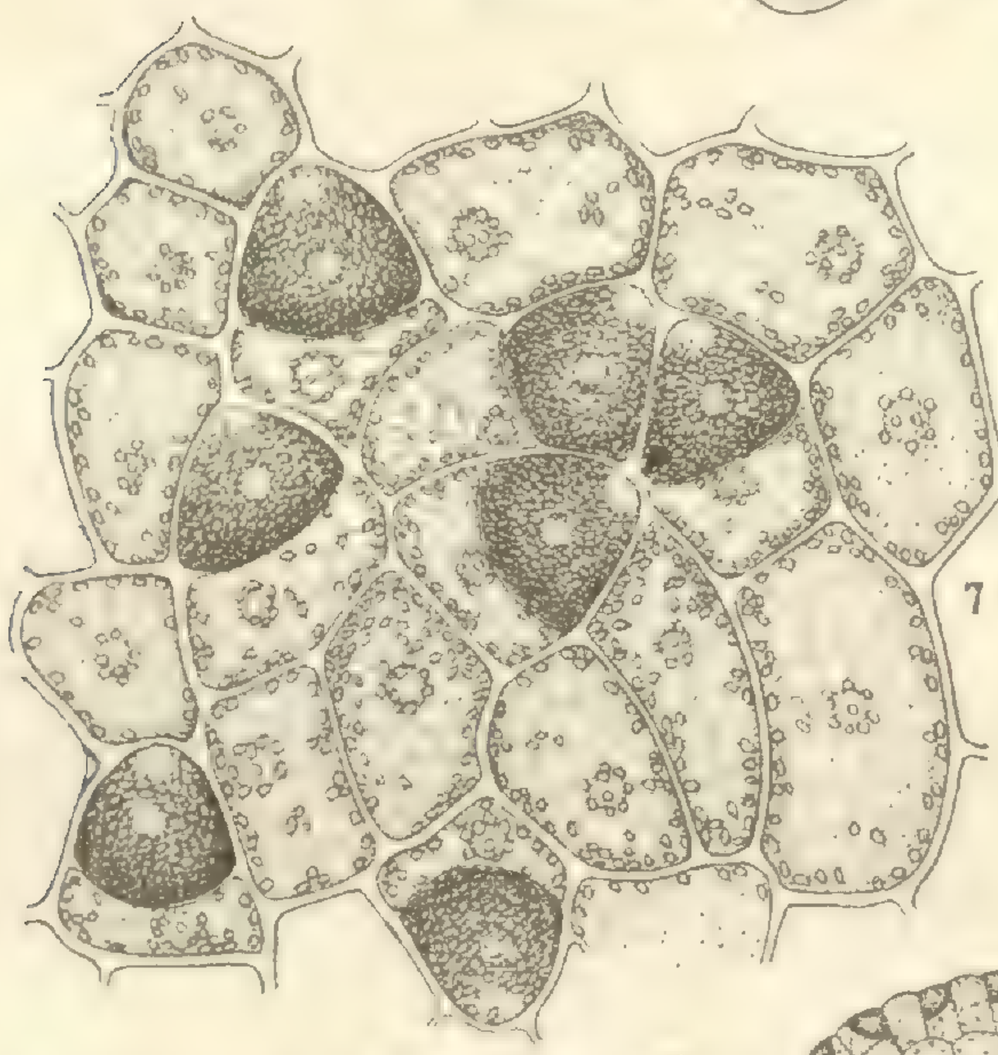
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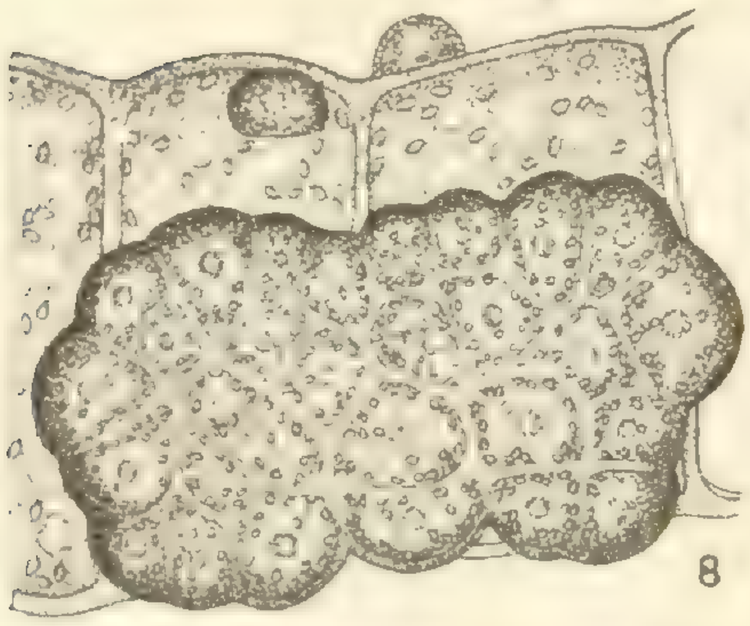
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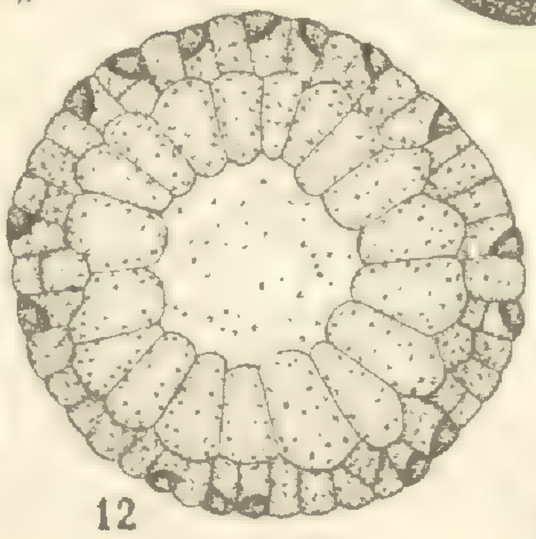
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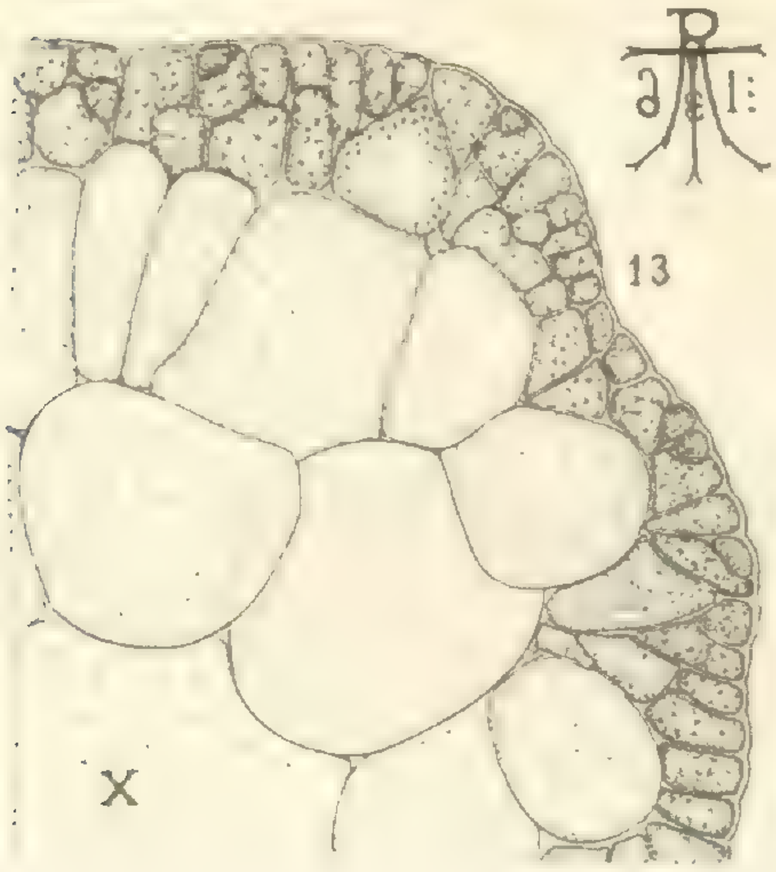
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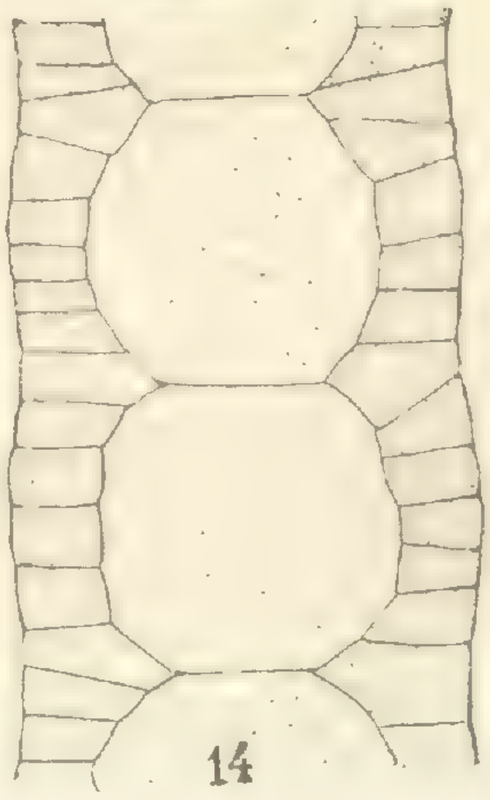
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EXPLANATION OF PLATE XXI.

The figures were drawn with camera, the following Zeiss objectives and eyepieces being used. *Figs. 1–6* and *9* obj. J (water immersion) oc. 4. *Figs. 7, 8* and *10* obj. J oc. 2. *Figs. 12–14* obj. A oc. 2. *Fig. 11* obj. D oc. 4. *Figs. 12* and *13* are drawn from the Daytona material, the remainder from that obtained at Cocoanut Grove. All the figures reduced about $\frac{1}{6}$ in photo-engraving.

FIG. 1. Portion of young filament showing three macroaplanosporangia.

FIGS. 2–6. Further development of the sporangium shown at the right in *fig. 1*, the macroaplanospore discharged in *figs. 5* and *6*.

FIG. 7. Portion of cortical layer of older filament with seven macroaplanosporangia in which the aplanospores are nearly mature.

FIG. 8. Surface view of sorus of microaplanosporangia.

FIG. 9. Microaplanospores.

FIG. 10. First stages in the formation of sori in younger filament.

FIG. 11. Small sori on younger filament.

FIGS. 12–13. Transverse section of older filaments showing multiple cortication. Some of the superficial cells have formed macroaplanosporangia.

FIG. 14. Longitudinal section of filament with simple cortication.

CULTURES OF UREDINEÆ IN 1899.[1]

J. C. ARTHUR.

WITH the exception of the very important results achieved by Thaxter in the study of American Gymnosporangia, together with similar work by Farlow, Halsted, Stewart, and Carver, only a few attempts have been made in America to trace the connection experimentally between the forms of the Uredineæ.

The three stages of the clover rust (*Uromyces Trifolii*) were shown by Howell to be genetically connected and the two forms of the raspberry rust (*Gymnoconia interstitialis*) by Clinton. A slight amount of work in this line of research, chiefly of a confirmatory character, was carried out between 1889 and 1898 by Bolley, Stuart, and the writer. The yet unpublished results of Carleton, obtained as part of the work of the division of vegetable physiology and pathology at Washington,[2] complete the mention of all American efforts in this line that now occur to the writer.

The cultures made during the present season (1899), herein to be described, were conducted, with the exception of a single trial, under glass in the greenhouses of the Experiment Station at Purdue University, and upon plants in pots, the plants remaining under cover until the observations were completed. Material bearing teleutospores of a number of species was collected during the previous autumn and winter and preserved until needed by tying in loose muslin and placing on the ground out of doors.

The method generally adopted to secure infection was the same, whether æcidia, uredo, or teleutospores were in hand. The potted plant was first wet with an atomizer, parts covered with a bloom being rubbed with the fingers until the water

[1] Read before the Botanical Section of the Am. Assoc. Adv. Sci., Columbus meeting, August, 1899.

[2] Issued as Bulletin No. 16 since the paper was read.

adhered. The spores were scraped from the host material with a knife blade and placed on definite areas of the plant to be infected, the parts marked by bits of string, and a bell jar placed over the whole plant. After a day or two the bell jar was removed. With most species, if the operation had been successful, the results began to appear in six to fourteen days.

In order that the simple procedure here outlined may uniformly give information that can be relied upon, many small precautions must be observed that cannot now be spoken of. In every case it is wise to first make a drop culture, to be sure that the spores are viable.

In the following outline of the work accomplished it is impossible to go into much detail, or mention all the items of interest that are naturally brought to mind. It is also impossible to adjust the nomenclature in accordance with the new knowledge which the cultures have furnished.

1. Puccinia Phragmitis (*Schum.*) *Körn.*

The host of this species, *Phragmites communis*, does not grow in the vicinity of Lafayette, Indiana, where the work was done, and I am indebted to Dr. J. J. Davis of Racine, Wis., and Professor C. E. Bessey, of Lincoln, Neb., for teleutosporic material. Abundance of æcidia were obtained by sowing the teleutospores upon *Rumex crispus* and *R. obtusifolius*, thus confirming the results obtained by European investigators. The dates are as follows:

May 2, Teleutospores (Wis.) sown on *Rumex crispus*; May 12 spermogonia; May 15, æcidia.

May 4, Teleutospores (Wis.) sown on *Rumex obtusifolius*; May 15, spermogonia; May 16, æcidia.

May 9, Teleutospores (Neb.) sown on *Rumex crispus*; May 15, spermogonia; May —, æcidia.

May 9, Teleutospores (Neb.) sown on *Rumex obtusifolius*; May 15, spermogonia; May —, æcidia.

The preliminary drop cultures showed the most vigorous germination of teleutospores obtained with any species, and far surpassing most of those under observation. The sowings also

produced a wealth of æcidia. From these facts one would infer that æcidia on Rumex should be common, for the teleutosporic condition occurs throughout the United States. Yet I am not aware of a single authentic record of *Æcidium rubellum* being found in North America. To be sure, it occurs in the earliest published list of American fungi by Schweinitz, who was a notably accurate observer. But his remark that the spots were usually sterile, makes it fairly certain that what he collected were not æcidia, but the spots made by *fungi imperfecti*. Both Professor Bessey and Dr. Davis at my suggestion made repeated and thorough search about the places where the teleutospores were found in their localities, but saw no æcidia. Improbable as it may seem, there yet appears to be no explanation of the remarkable vigor of this heteroecismal species, but to suppose that the æcidia do occur in America, and that, so far, they have been overlooked.

2. Puccinia Convolvuli *Cast.*

The teleutospores of this very common species of rust on *Convolvulus sepium* were sown on the host, before the weather permitted it to start out of doors, and were duly followed by a rich development of spermogonia and subsequently of æcidia. It was thus experimentally shown to be an autœcious species, as has always been tacitly accepted. The dates are as follows:

May 8, Teleutospores sown; May 16, spermogonia; June 6, æcidia.

3. Puccinia Caricis (*Schum.*) *Reb.*

The æcidiospores from *Æcidium Urticæ* were sown May 17 on the young leaves of *Carex stricta* and in eleven days were followed by uredospores. A sowing at the same date on *Carex cephalophora* gave no infection. This shows that *Carex stricta* is a host for *Puccinia caricis*, but there is reason to believe that it also acts as a host for other species of Puccinia. The American rusts on Carex are yet little understood.

4. Uromyces Euphorbiæ *C. & P.*

There has been an almost uniform opinion among American botanists that the Æcidium occurring abundantly upon many

species of Euphorbia is not genetically related to the brown rust equally abundant upon the same hosts. The evidence I have to offer is not conclusive, but, so far as it goes, must change this view. On June 20 æcidiospores from *Euphorbia nutans* were sown upon two plants of the same species and upon one plant of *Euphorbia maculata*. Nine days afterward uredo appeared upon one of the plants of *Euphorbia nutans*, and in eleven days upon the other, followed in both cases by teleutospores after a time, the exact date not recorded, but the plant of *E. maculata* showed no infection.

Instead of speculating upon such meager data, I am inclined to believe that *Uromyces Euphorbiæ* is an autœcious species, and to await further cultures showing if it is separable into races.

5. Phragmidium speciosum *Fr.*

The intimate association of a cæoma, which is not distinguishable from *Cæoma miniata* Schl., with this exclusively American species of Phragmidium, would have been accepted as sufficient evidence of its genetic connection, if the same form apparently had not been considered in Europe as the first stage of the very different *Phragmidium mucronatum*, a species that is also common in this country.

At the time when the teleutospores of *Phr. speciosum* were in germinating condition no potted plants of native roses were available, and sowings were made upon the leaves of a tea rose, the Kaiserin Augusta Victoria. The work was done by my assistant, Mr. William Stuart, and the dates are not at hand, but in due course of time many pustules of cæoma appeared. These bore every resemblance to the usual form, although they did not become very large, which may have been due to the host not being congenial.

It is probably safe to assume that the rose cæoma in this country belongs wholly to *Phragmidium speciosum*, or else that there are two species not at present separable.

6. Triphragmium Ulmariae (*Schum.*) *Lk.*

This species of rust, not heretofore reported for America, so far as the writer knows, was found in considerable abundance

this spring near Lafayette, Ind., upon *Ulmaria rubra* (*Spiræa lobata*), in the bright red cæoma stage. Feeling at first uncertain of the identity of the rust, the cæoma spores were sown upon the Ulmaria, and also upon Salix, Convolvulus, and Ipomœa, with the result that it grew only upon Ulmaria, producing at first uredospores and afterward teleutospores. An after-sowing of uredospores upon Ulmaria gave a crop of more uredospores. The dates are as follows:

May 17, Cæomospores sown on *Ulmaria rubra;* May 30, uredo; July — teleutospores.
May 17, Cæomospores sown on *Salix longifolia;* no infection.
May 23, Cæomospores sown on *Convolvulus sepium;* no infection.
May 24, Cæomospores sown on *Ipomæa pandurata;* no infection.
June 16, Uredospores sown on *Ulmaria rubra;* July —, uredospores.

7. Puccinia Americana *Lagh.*

This grass rust on various species of Andropogon is very common throughout North America, but has been generally confounded with *Puccinia Andropogi* Schw., which has the same range and affects the same hosts. The teleutospores are barely distinguishable, but the uredospores are entirely unlike those of *P. Americana*, being large and thin walled, those of *P. Andropogi* small and thick walled. The detection of the æcidium is due to the careful observation of Mr. William Stuart, who noticed that plants of *Pentstemon pubescens*, growing near Andropogon bearing teleutospores of the previous year, were well covered with æcidia (*Æcidium Pentstemonis* Schw.), while the same species in other localities was quite free. With this hint sowings were undertaken. Teleutospores from *Andropogon scoparius* were sown on *Pentstemon pubescens* and æcidia appeared in great abundance and vigor; æcidiospores were sown on Andropogon and large, thin-walled, brown uredospores appeared. The results were ample and complete, and were further emphasized by similar results subsequently obtained by Mr. Stuart. The dates are as follows:

May 3, Teleutospores from *Andropogon scoparius* sown on *Pentstemon pubescens;* May 11, spermogonia; May 20, æcidia.

May 4, Teleutospores from *A. furcatus* sown on *Œnothera biennis*; no infection.

May 15, Æcidiospores from *P. pubescens* sown on *A. scoparius*; May 29, uredo.

8. Puccinia angustata *Pk.*

The detection of the æcidium of this common rust on Scirpus was also due to a fortunate observation. It was noticed that some plants of Lycopus, growing within a few feet of *Scirpus atrovirens* covered with last year's teleutospores, were well besprinkled with æcidia (*Æcidium Lycopi* Ger.), while plants some distance away were free. Sowings of æcidia were made on the leaves of the Scirpus and characteristic uredo obtained. The hint was secured so late in the season that only one sowing was possible, but the result is thought to be measurably reliable.

May 23, Æcidiospores from *Lycopus Americanus* sown on *Scirpus atrovirens*; June 6, uredo.

9. Puccinia Windsoriæ *Schw.*

This rust occurs, often in great abundance, upon the much benamed grass, *Triodia cuprea* (*Sieglingia seslerioides* Scrib.), which in the days of Schweinitz was standing in the genus Windsoria. The name of the rust was applied in Burrill's *Parasitic Fungi of Illinois* fourteen years ago, to the very different rust on Muhlenbergia, hence great confusion has arisen, and in nearly all recent lists and treatises the name is misused.

The hint that led to successful cultures came from an observation upon proximity, as in the previous cases. A small shrub of *Ptelea trifoliata* was made conspicuous by the bright yellow spots of *Æcidium Pteleæ* B. & C., and not ten feet away was a large clump of the grass with the dead stems and leaves black with teleutospores. Successful sowings of æcidiospores were made on the grass, but the season by this time had advanced so far that germinating teleutospores were no longer obtainable with which to try the reverse cultures. The dates are as follows:

May 15, Teleutospores sown on *Ambrosia trifida*; no infection.

May 17, Teleutospores sown on *Napæa dioica*; no infection.

June 8, Æcidiospores sown on *Triodia cuprea*; June 15, uredo.

June 16, Æcidiospores sown on *Triodia cuprea*; June 23, uredo.

10. Puccinia Vilfæ *A. & H.*

This species of rust, better known as *P. Sydowiana* Diet., is necessarily restricted in the vicinity of Lafayette to the few localities where the host, *Sporobolus longifolius*,[3] is to be found. My attention was called to the fact by Miss Lillian Snyder that in such localities the exceedingly common upright verbenas were richly covered with *Æcidium verbenicola* K. & S., and with no other species of æcidia in the vicinity. Going over the ground myself, I found that the verbena plants, *Verbena stricta* being particularly abundant, were more thickly studded with æcidia the closer they stood to tufts of rusted Sporobolus, and that fifty feet away from such source of infection they would be entirely free.

Cultures were undertaken in 1898, but too late in the season to secure results. In the mean time a morphological resemblance was observed between the spores of *Æcidium verbenicola* and the uredospores of *Puccinia Vilfæ*, that gave another hint at genetic relationship. Both sorts of spores were approximately obovate, with colorless walls, greatly thickened at the apex, and papillose instead of echinulate. Successful cultures have shown that these rather uncommon characters meant more than a coincidence in this case. It is the first time, so far as the writer knows, that any significant resemblance has been pointed out between the spores of æcidia and uredo of the same species.

For some unexplained reason I was unsuccessful in germinating the teleutospores of *P. Vilfæ*, although they were taken a number of times directly from the field. But with æcidiospores the results were ample and convincing. The dates are as follows:

May 31, Æcidiospores from *Verbena stricta* on *Sporobolus longifolius*; June 10, uredo.

June 9, Æcidiospores from *Verbena stricta* on *Sporobolus longifolius*; June 21, uredo.

[3] Since this paper was read I have discovered that the grass under observation was *Sporobolus longifolius* (Torr.) Wood, instead of *S. asper*, as given in the manuscript, and printed in Science **10**: 565, and Proc. A. A. A. S. **48**: 299. The latter grass does not grow in this region.

11. Puccinia peridermiospora (*E. & T.*) *Arth.*

In studying the grass rusts it was noticed that a form on Spartina, well represented in American herbaria and usually called *Puccinia Phragmitis*, had uredospores similar to those of *Puccinia Vilfæ*, just described. I searched through my collection of Æcidia to see if any species with corresponding apically thickened spores could be found, and was rewarded in the case of *Æcidium Fraxini* Schw. With this morphological hint as the sole guide cultures were undertaken.

Spartina does not grow within many miles of Lafayette, and I am indebted to the kindness of Professor C. E. Bessey, of Lincoln, Neb., and Mr. H. H. Hume, of Ames, Iowa, for teleutosporic material upon *Spartina cynosuroides*. The teleutospores germinated with marked vigor, and were first sown on *Ptelea trifoliata*, the small plants obtained being mistaken for Fraxinus. When the mistake was discovered, and sowings were made on *Fraxinus viridis*, infections were first secured. As no small plants of Fraxinus were available, the spores were sown upon cut twigs placed in water in the greenhouse, and upon a low branch of a large tree out of doors. There could be no fear of spontaneous infection, as the species does not occur in the region, either upon Spartina or Fraxinus, but the usual precautions were taken. The sowings were both successful. The dates are as follows:

May 8, Teleutospores (Neb.) sown on *Ptelea trifoliata*; no infection.
May 9, Teleutospores (Neb.) sown on *Ptelea trifoliata*; no infection.
May 9, Teleutospores (Iowa) sown on *Ptelea trifoliata*; no infection.
May 15, Teleutospores (Neb.) sown on *Ptelea trifoliata*; no infection.
May 17, Teleutospores (Iowa) sown on cut twigs of *Fraxinus viridis*; May 24, spermogonia; June 6, æcidia.
May 17, Teleutospores (Neb.) sown on tree out of doors of *Fraxinus viridis*; May 29, spermogonia; June 8, æcidia.

SUMMARY.

The following are the eleven species of Uredineæ, whose æcidial and teleutosporic forms have been definitely connected by cultures:

1. *Puccinia Convolvuli* Cast. and *Æcidium Calystegiæ* Desm. with sowings of teleutospores.
2. *Puccinia Phragmitis* (Schum.) Körn. and *Æcidium rubellum* Pers. with sowings of teleutospores.
3. *Puccinia Americana* Lagh. and *Æcidium Pentstemonis* Schw. with sowings of æcidiospores and teleutospores.
4. *Puccinia Windsoriæ* Schw. and *Æcidium Pteleæ* B. & C. with sowings of æcidiospores.
5. *Puccinia Vilfæ* A. & H. and *Æcidium verbenicola* K. & S. with sowings of æcidiospores.
6. *Puccinia peridermiospora* (E. & T.) Arth. and *Æcidium Fraxini* Schw. with sowings of teleutospores.
7. *Puccinia Caricis* (Schum.) Reb. and *Æcidium Urticæ* Schum. with sowings of æcidiospores.
8. *Puccinia angustata* Pk. and *Æcidium Lycopi* Ger. with sowings of æcidiospores.
9. *Uromyces Euphorbiæ* C. & P. and *Æcidium Euphorbiæ* Am. Auct. with sowings of æcidiospores.
10. *Phragmidium speciosum* Fr. and *Cæoma miniata* Am. Auct. with sowings of teleutospores.
11. *Triphragmium Ulmariæ* (Schum.) Lk. and *Cæoma Ulmariæ* Thüm. with sowings of æcidiospores and uredospores.

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BRIEFER ARTICLES

ORIGIN OF THE THALLUS, ALTERNATION OF GENERATIONS, AND THE PHYLOGENY OF CUTLERIA.[1]

The Cutleriaceæ (Cutleria and Zanardinia) may be considered among the most interesting and remarkable forms of the Phaeosporeae.

The two fronds, sexual and asexual, of the single species of Zanardinia (*Z. collaris*) are identical. The genus Cutleria, represented in Europe by two species, has a sexual thallus whose structure and development is very different from the asexual form. The oogonia and antheridia are borne upon the plant named Cutleria, whose thallus is composed of and formed through the union of marginal filaments remaining free upon the periphery, and becoming divided by partitions with the thickening of the thallus following the fusion. So the thallus is both a pseudoparenchyma and a true parenchyma.

The sporangia are borne in the upper surface of Aglaozonia, which has a creeping habit, and grows by marginal cell division like Zonaria. It now seems to be established that *Aglaozonia parvula* is the asexual form of *Cutleria multifida*, and one may suppose with Falkenberg that *A. chilosa* is the asexual form of *C. adspersa*. In reality, however, this supposition rests upon the fact that we do not know in Europe any other species of Cutleria or Aglaozonia.

But I have found at several points on the coast of the gulf of Gascony a new Aglaozonia, the *Zonaria melanoidea* of Schousboe, discovered at the beginning of the century at Maroc, and not reported since, whose Aglaozonia nature has remained unrecognized. For various reasons I consider *Aglaozonia melanoidea* to be the sporophyte of *C. adspersa*. If that form has not been seen up to the present in the Mediterranean where *C. adspersa* is not rare, it is without doubt because of its very great resemblance to Ralfsia. But since we do not know the gametophyte of *A. chilosa*, and as the Cutlerias are plants with a rather large thallus, conspicuous and easily recognized, it is

[1] This contribution is in part a résumé by Professor Sauvageau of his paper entitled "Les Cutleriaceæ et leur Alternance de Générations," Ann. d. Sci. Nat., Bot. 10: 265. 1899. Translated by Dr. Bradley M. Davis.

improbable that the Mediterranean hides a third species of Cutleria. Therefore *A. chilosa* multiplies always non-sexually, without alternation of generation, as is also the fact with *A. parvula* in northern Europe. If it possesses a gametophyte it is without doubt some exotic species (*C. compressa, C. pacifica*) as yet insufficiently studied.

As for the culture of oospheres of Cutleria, it has given up to the present very conflicting results. Thus in the middle of the century Thuret obtained through the germination of parthenogenetic oospheres some small plants somewhat resembling an Ectocarpus, which no one has since found, and which I call form *Thuretiana* of germination. But Falkenberg has obtained from the germination of fertilized oospheres (the only ones that did germinate in his cultures) some strange plants, at first with the form of a small upright column, at the base of which is borne, after it has arisen, a creeping plate comparable to Aglaozonia; these plants I call form *Falkenbergiana*. There is also a form *Falkenbergiana* that has been obtained by Church, but from the germination of parthenogenetic oospheres, in this respect differing from the results of Thuret and Falkenberg. Finally the zoospores of *A. parvula* have given to Church plants which, like the preceding, have the creeping plate-like thallus of Aglaozonia, but whose column ends at the summit in filaments (not fascicled) which bear the reproductive organs of Cutleria. I have named this new example of germination form *Churchiana*. Some plants comparable to these have developed in the cultures of Kuckuck.

How shall such divergent results be reconciled? It may always be borne in mind that the preceding authors have never obtained uniformity of germination in their cultures.

Now I have found *C. adspersa* at Guéthary (Basses-Pyrénées) when the male plants were more numerous than the female. The discharge of the sexual elements was abundant, and took place readily in my cultures. However, I have never obtained fertilization; the oospheres did not even attract the antherozoids. At times they germinated very readily parthenogenetically and gave always and characteristically the form *Falkenbergiana*. This is in agreement with the observations of Church, but my results are the more surprising, for the English author found only a few or no male plants; his female plants were therefore unfortunately parthenogenetic.

It occurred to me to look for germination of spores in nature upon the Cutleria plants themselves. I have found a great many of the

sporelings *Thuretiana* and *Falkenbergiana* and rarely some *Churchiana*. One finds all the intermediate conditions between very young *Thuretiana* in the form of a simple filament, and young Cutleria fascicled or with free filaments at the margin; consequently the form *Thuretiana* gives rise to the thallus of Cutleria, and is not an abnormality of the cultures as Falkenberg believed. The sporelings *Falkenbergiana* were truly thalloid, and I have shown that the column takes on a larger thallus than would be supposed from the cultures of the preceding authors. I was able to follow sufficiently far the development of the creeping Aglaozonia-like plate whose structure resembles that of *A. melanoidea*.

This is, therefore, the first time that these plants have been found united, but what of their origin? They cannot be attributed to the zoospores of *A. melanoidea*, for during all the time of my observations these plants remained sterile. Since the parthenogenetic oospheres in my cultures of Cutleria gave on germination form *Falkenbergiana*, it is to be supposed that identical plants found in nature in the same locality and at the same time would have the same origin. And since in this situation the male individuals are more numerous than the female, one may admit the antherozoids should play a part, and that fertilization, although not operative in my cultures, occurs in nature, and consequently that the form *Thuretiana* owes its development to fertilized oospheres. As for the form *Churchiana*, that is an anomaly, an example of *Falkenbergiana* with the column changed at the tip into Cutleria; it is interesting in the same manner as a flower of some phanerogam with metamorphosed petals and stamens.

If the results obtained by previous authors are reconciled, we must acknowledge from these conclusions that alternation of generations is not necessary, but rather, as one may say, facultative. Moreover, an oosphere of Cutleria, whether it be parthenogenetic or fertilized, may give on germination either Cutleria or Aglaozonia. Similarly, a zoospore of Aglaozonia may produce Cutleria or Aglaozonia. But we do not know the conditions that govern the development from the zoospores or oospheres in either case.

As for the affinities of Cutleria, they are numerous. The sexual thallus (Cutleria proper) has a method of development that is found in the Sporachnaceæ; it bears oogonia and antheridia similar to those of Sphacelariaceæ and Tilopterideæ. The asexual thallus (Aglaozonia) recalls certain of the Sphacelariaceæ (Battersia, *Sphacelaria olivacea*) and certain of the Dictyotaceæ (Zonaria, Padina).

But Aglaozonia is not a direct product of germination ; it is a secondary product, always formed from a pro-embryo or small column. Now the column produces normally at its base the creeping thallus of Aglaozonia, and abnormally at its tip a frond of Cutleria (form *Churchiana*). Here are the extremes, Cutleria and Aglaozonia, but the column has a place between, although its structure differs clearly from both. It appears to us to be a necessary and fundamental organ, probably of great importance phylogenetically. In its structure the column resembles greatly those of Myriotrichia and Litosiphon ; it is possible that in teratological conditions it forms reproductive organs, which knowledge would throw strong light upon its affinities. I consider Cutleria, therefore, as a union of three genera, Cutleria proper, Aglaozonia, and the column of some unknown genus.—C. SAUVAGEAU, *University of Dijon, France.*

SOME PLANTS OF NEW MEXICO.

CASTILLEIA CONFUSA × ACUMINATA, n. hyb.—Leaves variable, some just as in *C. acuminata*, others on the same plants very narrow, almost linear, as in *C. confusa ;* bracts with lateral narrow lobes 3 to 4^{mm} long in the dried plant (1–1.5^{mm} in *acuminata*, at least 4^{mm} in *confusa*) ; apical parts of bracts delicately tinted with pink (yellow in *acuminata*, bright red in *confusa*) ; galea 6^{mm} (8^{mm} in *confusa*, hardly 5^{mm} in *acuminata*) ; plant rather rougher than *acuminata.*

Harvey's Ranch, near Las Vegas, New Mexico, 9600^{ft}, August 22, 1899. (*Wilmatte Porter* and *T. D. A. Cockerell*). This is clearly a hybrid, and was found growing in a meadow along with quantities of *C. confusa* Greene, and *C. acuminata* (Pursh).

SIDALCEA CANDIDA **tincta**, n. var.—Similar to *S. candida*, but petals suffused with pink toward their ends ; anthers before dehiscence bright pink : on dehiscence turning black ; pollen white ; petals barely emarginate, 12^{mm} long, 10.5 broad ; calyx lobes broad at base, narrow at apex, pointed, about 6^{mm} long and 3^{mm} broad at base ; cauline leaves a rather light bright green, palmately 5 to 7-parted, or cleft nearly to the base, the divisions about 60^{mm} long and 17^{mm} broad, on the upper leaves entire, on the lower 2 or 3-cleft at the ends ; stem light green, shining, glabrous ; calyx and peduncles rough and more or less hairy ; carpels 8, smooth when ripe, with an upright hairy beak.

Harvey's Ranch, near Las Vegas, N. M., 9600ft, July 25, 1899 (*Flora Beschle*) and August 22, 1899 (*Cockerell*). This is a distinct looking plant, but it represents only a peculiar local tendency, not a separate specific type.

SIDALCEA NEOMEXICANA Gray.—Good material of this, from Las Vegas, N. M., and elsewhere, has the mature carpels strongly reticulated. I thought I had a new species, but it is evidently only *neomexicana*. In the herbarium of the N. M. Agricultural College, Professor E. O. Wooton has specimens showing smooth and reticulated carpels, collected at the same time and place.

CLEMATIS OCCIDENTALIS[2] **albiflora,** n. var.—Sepals white.

Common at Beulah, New Mexico (*W. Porter; Cockerell*), where the typical form, with purplish-blue sepals, is rare.

CALOCHORTUS GUNNISONI **perpulcher,** n. var.—Petals larger, 40–42mm long and 45mm broad, pale primrose yellow, a large purple basal spot, irregular purplish bands as in type, transverse gland yellow, about 10mm diameter, the breadth of the petal at this level being 18mm; style blue; stigma pale sea-green, with dark mottling; anthers pale yellow; petals almost white beneath, greenish and finely streaked with dark blue on basal portion; sepals colored like basal half of petals.

Harvey's Ranch, near Las Vegas, N. M., July 25, 1899 (*Flora Beschle*); Beulah, N. M. (*Wilmatte Porter*). This stands out well from the typical *C. Gunnisoni* of Colorado, which grew all round my former place of residence in that state.—T. D. A. COCKERELL, *Mesilla Park, New Mexico.*

[2] *Atragene occidentalis* Hornem. Hort. Hafn. 520. 1813.

CURRENT LITERATURE.

BOOK REVIEWS.

Bailey's Cyclopedia.[1]

In America there has been but one cyclopedic work on horticulture, viz., Henderson's *Handbook of Plants*, published in 1881, with a second edition in 1890, each edition in one volume. Accordingly, botanists, as well as horticulturists, have been looking forward with eagerness to the appearance of Professor Bailey's great work. The opening paragraph of the preface tersely states its purpose: "It is the purpose of this work to make a complete record of the status of North American horticulture as it exists at the close of the nineteenth century. The work discusses the cultivation of fruits, flowers, and garden vegetables, describes all the species which are known to be in the horticultural trade, outlines the horticultural possibilities of the various states, territories, and provinces, presents biographies of those persons, not living, who have contributed most to the horticultural progress of North America, and indicates the leading monographic works relating to the various subjects."

Only Professor Bailey would have undertaken this tremendous task. It is probable that no one, excepting the editor and his immediate associates, can appreciate the amount of detail which such a work must involve. The editor has set down some of the items as follows: "More than 10,000 species of plants in cultivation; almost every important species phenomenally variable, sometimes running into thousands of forms; every species requiring its own soil and treatment, and sometimes even minor varieties differing in these requirements; limitless differences in soils and climates in our great domain, every difference modifying the plants or their requirements; a different ideal in plant-growing and plant-breeding in the mind of every good plant-grower; as many different kinds of experience as there are men; many of these men not facile with the pen, although full of wholesome fact and experience; the species described in books which deal with the four corners of the earth; very few botanists who have given attention to the domestic flora." The editor has said that "the most difficult part of the making of a cyclopedia is to project it. Its scope and point of view must be determined before a stroke of actual work is done. This much done, the remainder is labor

[1] Bailey, L. H.—Cyclopedia of American Horticulture. Assisted by Wilhelm Miller and many expert cultivators and botanists. Illustrated with over 2000 original engravings. In 4 vols. Vol. I. A–D. 4to. pp. xxii + 509. New York: The Macmillan Company. 1900. $5.00.

rather than difficulty." For more than ten years Professor Bailey has been moving in the direction of this cyclopedia, much of his published work in the meantime being "material on the way" to the larger venture. The "Annals of Horticulture," published for five years, was the first tangible result, "designed to be a witness of passing events and a record of progress."

To compile a cyclopedia by using other cyclopedias involves drudgery, but presents no special difficulties, and results in no special merits. In Bailey's *Cyclopedia*, however, the work is new from start to finish, both in text and illustrations, and the list of collaborators shows that the most expert assistance has been obtained.

The illustrations, too, deserve special mention for the happy combination of scientific and artistic excellence, and it has been one of the rules of the "make up" that "wherever the book opens an engraving will be seen." Besides, the book is distinctly American in its flavor, fully setting forth American experience and conditions.

The matter may be arranged under three heads: cultural, taxonomic, and morphological, and the sequence seems to express their relative importance, as "the stress is laid upon the plants as domesticated and cultivated subjects."

In reference to the cultural parts the reviewer can express no opinion, but botanists are familiar with Professor Bailey's standard in such matters, and need no assurance as to the freshness and vigor of this portion of the work.

The following example, under the title *Acacia*, will serve to illustrate the taxonomic portion of the work. The genus is described briefly, in language as non-technical as possible, and a synopsis of fifty-three species is given, including all those in the American trade. The synopsis consists of an analytical key, brief descriptions, and essential synonymy, just as in an ordinary manual, so that the *Cyclopedia* becomes a great manual for all plants in cultivation in America.

The morphological titles, such as "flower," etc., are to appear chiefly in subsequent volumes, and comment on this topic will be deferred.

To the botanist the *Cyclopedia* is a mass of most valuable information, bringing together, as it does, into available and properly edited form, the immense contribution of facts from horticulturists to the whole evolutionary doctrine, and enabling the morphologist to know what form he is handling and what has been done with it. The work should find its place in the libraries of all botanical laboratories as well as in those of practical horticulturists.—J. M. C.

Minnesota plant life.

FOR the second time botanists have had the pleasure of seeing a book that has for its topic the vegetation of one of our states. Pound and Clements'

Phytogeography of Nebraska was a work that marked a distinct advance in the ecological investigation of our country. MacMillan has now given us an attractive presentation of the plant life of Minnesota.[2] The purpose of this work, however, is different from that of the earlier one. Its style is less technical and the pages abound in illustrations. The author distinctly states that his purpose is the botanical education of the people of Minnesota, not through the use of the book as a text, but rather through its intelligent perusal by the wide-awake boys and girls of the state. The author remarks that the book is more the offspring of the woods and lakes than of the laboratory and library. The work, then, is to be judged from the standpoint of the people rather than from the standpoint of the botanist, although Professor MacMillan endeavors to make the book scientific as well as popular.

The introductory chapter deals with the relation of the Minnesota flora to that of the whole country, and the author gives a brief discussion of the forest and prairie with their lines of tension. Then follows a chapter on the wanderings and migrations of plants. Most of the book (390 out of 525 pages) is taken up with a popular and readable description of the plants of the state, beginning with the slime-molds and closing with the composites. Common names are given in most instances, even if they have to be introduced for the occasion, as in the case of many of the lower forms. The cryptogams are given great prominence, and are well illustrated by a number of excellent half tones. The feature of this part of the work is the untechnical description of the various species. In most cases the ecological and economic relations of the plants are most fully treated, as they should be in a work of this kind. More technical chapters are also introduced for those who are interested in the philosophy of the subject; such chapters are those that deal with alternation of generations and the meaning of the seed habit.

The latter part of the book is distinctly ecological, treating the adaptations of plants to their surroundings and also the plant societies in the familiar way. The last two chapters are physiological, dealing with nutrition and reproduction.

This work does not pretend to be an addition to science, although many of the photographs may be regarded as contributions along this line. The wealth of illustration is one of the strongest features of the book and it is doubtless superior in this regard to any work that has yet appeared in America. Not only are the illustrations numerous, but they show what they are said to show, which is not true of all illustrated books. The style is very

[2] MACMILLAN, CONWAY: Minnesota Plant Life. Report of the Survey, Botanical Series III. Imp. 8vo. pp. xxv + 568. *pl. 4. figs. 240.* St. Paul, Minn.: Published by authority of the Board of Regents of the University for the People of Minnesota. 1899.

attractive and must appeal not only to the botanical reader but to all who have a love for nature. The book abounds in catchy phrases and presents plants almost as though they were human. One result of the study of this book ought to be a more widespread recognition of plants as living things, which have rights to be respected.

Adverse criticisms upon *Minnesota Plant Life* are few, and are mainly incident to the popularization of a scientific subject. However, it is very doubtful whether a book of this character is the place in which to exploit such ideas as these: peat bog plants have xerophytic structures so as to prevent the rapid passage of water through the tissues (p. 436); the inclusion of salvinias and bladderworts under the term plankton (p. 443); extreme views on the significance of colors, in which blue as well as red is called a "warming-up" color, so that blue and red flowers are said to come from northern climes and yellow flowers from warmer climes, and that spring and fall flowers are blue or red, while summer flowers are yellow (p. 426); vernal plants are said to have come from the north, and the more leisurely plants from the south; sunflowers and their allies are the highest of the plants and may form the forests of the future (p. 471). All of these ideas are extremely fanciful, if not untrue. They may properly have a place in poetry and in the graduate classes in ecology; but the popular mind is already too full of such ideas, and it seems a pity that botanists should further encourage this kind of thinking by using it in popular works.— HENRY C. COWLES.

A popular treatise on bacteria.

IN ONE of the recent volumes of the Science series the author, Mr. George Newman, attempts "to set forth a popular scientific statement of our present knowledge of bacteria."[3] The following are the principal topics discussed: the biology of bacteria; the bacteria of water, air, and soil; bacteria in milk and other foods; bacteria in fermentation; immunity and antitoxins; bacteria and disease; and disinfection. This list of subjects is an attractive one. The literary style is easy and in many ways the book seems to possess those qualifications which will assure for it a ready sale.

Books on popular science, especially if pleasing in style and manufacture, reach a vast number of readers and form a very important educational factor. Often a single book is the only treatise upon a given subject that falls into the hands of the reader. In such instances the book stands as an "authority" in the reader's mind. Because of this exalted position, which may be reached by the popular treatise with or without good reason, such books may properly be subjected to even more searching criticism than are more abstruse texts.

[3] NEWMAN, GEORGE: Bacteria, especially as they are related to the economy of nature, to industrial processes, and to the public health. 8vo. pp. xiv + 348; *illus.* New York and London: G. P. Putnam's Sons. 1899.

This is all the more necessary since they are intended for a class of readers who are incapable of sifting the true from the false.

In the book in hand statements similar to the following are frequent. "Many species . . . . rise to the surface and lodge in the pellicle to form their seeds" (p. 19). Such a use of the word "seed" is unwarranted even in a popular treatise. On page 16 may be found this erroneous statement: "*Micrococcus agilis* is the only coccus which has flagella and active motion." On page 36 the word "attenuated" is used in such a way as to lead the unwary to believe that attenuation is synonymous with decrease in vegetative power. *Bacillus tuberculosis* is a well-known example of an organism which decreases in virulence as it increases in vegetative power in artificial culture. On page 68 is given a very questionable method for the diagnosis of cholera, viz., the direct examination of flakes of detached epithelium.

As types of loose or misleading sentences, which are very common, may be noted the following: "It will be understood that bacteria do not live in air" (p. 107), a statement that quite fails to express the meaning intended. "The gases (!) essential to plants are four, carbon dioxide, hydrogen, oxygen, and nitrogen" (p. 146); and again on p. 147, "Here then we have the necessary food of plants expressed in a sentence: *water, gases, salts, the most important and essential gas and some of the salts being combined in nitrates.*" "The reduction of a nitrite is a common property of bacteria" (p. 150). The expression "organismal process" (p. 29) is surely very unusual. "Pure cholera bacillus in suspension and typhoid bacillus in suspension were passed through these filters and not a single bacillus was detectable in the filtrate" (p. 80). While this loose diction may not lead to error, it does cost the reader much time to discover the intended meaning.

On the whole, the book is like so many other popular works, a mixture of good and bad, the accurate and the misleading. Because of the looseness and the actual error it can only be commended to the discriminating student, for whom, least of all, it was intended and who needs it least. For popular reading a better book is necessary.—F. L. STEVENS.

The forestry problem.

THE announcement that Yale University is to have a school of forestry, and the appearance of a number of publications dealing with different phases of the forestry question, show that the crusade for a better understanding of the problem is having its effect. A recent work by Mr. Bruncken on North American forests and forestry[4] is not intended to be a guide for the professional forester, but rather to make clear to the general reader the exact condition of affairs. It is written for those who take a living interest in all

[4] BRUNCKEN, ERNEST: North American forests and forestry. Their relation to the national life of the American people. 8vo. pp. 262. New York: G. P. Putnam's Sons. 1900.

questions affecting the welfare of the nation, and who love the life of nature without standing apart from the more strenuous current of human affairs.

The chapter on the North American forest contains an excellent résumé of distribution of forests before they were changed by the influence of man. It is shown that the forest is controlled by certain definite factors and that the struggle of the forest with the prairie and the bog is constant, as is also the struggle between the individual trees of the same forest; so that a correct understanding of the complex conditions which determine the distribution of trees becomes of utmost importance in silviculture.

The next chapter contains a brief history of the relation of the forest to the growth of the nation. It was absolutely necessary for the pioneer to clear the forest, and the damage his immediate successors have done by carrying this destruction too far must be repaired by the present generation. The author takes a very optimistic view of the future condition of the forests.

Forest finance and management, forestry and government, protecting forests from fires and thieves, and forestry and taxation are so treated as to show that the author is well informed on these phases of the forestry problem. In chapters on reform in forestry methods, and forestry as a profession, a brief history of the reform is given and some mistakes are pointed out. Attention is called to the number of schools of forestry recently established, and to the practical results obtained by applying scientific methods to certain plots, which the Forestry Division of the U. S. Department of Agriculture is now encouraging owners to do.

The volume is not without literary merit; the author's style is clear and logical, and at times, as in the case of the description of a forest fire, fascinating. As the author well says, the question of forestry cannot be solved by sudden bursts of enthusiasm, and does not appeal to man's emotional nature. Sensible treatment of our forest wealth will come only through the education of the public along this line. The book deserves a wide reading because it will contribute to this end. — H. N. WHITFORD.

MINOR NOTICES.

IT IS a pleasure to receive a paper which possesses so many good qualities as the recension of the Mexican and Central American Umbelliferæ lately issued by Messrs. Coulter and Rose.[5] In examining this work one is impressed no less by its clear presentation of diagnostic and bibliographic essentials than by a judicious exclusion of irrelevant matter. The authors do not, for instance, attempt to give their work impressive proportions or an erudite appearance by adding under each genus and species all the synonymy which could have been cheaply compiled from the *Index Kewensis*

[5] COULTER, J. M. and ROSE, J. N.: A synopsis of Mexican and Central American Umbelliferæ. Proc. Wash. Acad. Sci. 1: 111–159. Jan. 1900.

If it seems best to give copious bibliography under one species, they do not feel it essential to cite for symmetry an equal amount of almost meaningless references under another.

The paper brings together in convenient form the results of considerable scattered activity, and the extent of recent work upon the group may be inferred from some introductory statistics. In 1880 Mr. Hemsley enumerated in the *Biologia Centrali-Americani* 25 genera and 76 species of Umbelliferæ. Messrs. Coulter and Rose — who, to the territory covered by Hemsley's work, add Lower California — recognize 39 genera and 182 species, including about 40 which are here described for the first time. It is interesting to note that this considerable increase in known species is about proportionate to the similar additions in the gamopetalous Mexican genera, which have been recently revised. It testifies not merely to the unforeseen wealth of the Mexican flora but also to the success of the many skilled collectors who, during the last two decades, have explored its vegetation with such diligence. Among these may be mentioned especially Messrs. Pringle, Palmer, J. D. Smith, Brandegee, Altamirano, Millspaugh & Gaumer, Nelson & Goldman, Rose, Hartman & Lloyd, L. C. Smith, Conzatti & González, C. L. Smith, Dugès, and Lamb.

The Umbelliferæ form a very natural group in which floral structure is remarkably constant. In their paucity of floral characters they may be compared to the Cruciferæ and, like them, have for the most part good species, comparatively few varieties, and (*exceptis neglectis*) technical rather than convincingly natural genera. It is a group, in fact, where numberless generic changes could be easily and plausibly initiated by anyone with a conscious or unconscious *penchant* for disagreement with his predecessors. The work of the present authors, however, is distinctly constructive rather than revolutionary.

In a paper where many names are cited a few slips are well-nigh inevitable; thus in the present instance *Seeman*, *Couthony*, and *A. L. Smith* have an unfamiliar look. The many specific names, which the authors have been obliged to coin, are mostly the simple and familiar descriptive terms of the *glauca*, *serrata*, and *rigida* type, with no such unscholarly linguistic jumbles as *pseudoparviflora*, *heterappendiculata*, *Saxifragopsis*, *parvicarpum*, etc., which have of late so frequently marred the publications from other American botanical establishments, although rarely found in the writings of our more classical transatlantic colleagues. Another point which merits special mention is the scrupulous care with which the authors have avoided the publication of manuscript or herbarium names in their synonymy — a useless practice which, notwithstanding the emphatic protest of Mr. B. Daydon Jackson and others, is still too prevalent.

The revision is illustrated by ten excellent plates and numerous text cuts. — B. L. ROBINSON.

PROFESSOR F. LAMSON-SCRIBNER has published the second part of his *American Grasses* as Bulletin 17 of the Division of Agrostology. It will be remembered that every species is illustrated. Part I contained illustrations of 302 species, and Part II adds 325. The interesting statement is made that of the 627 species now illustrated, "19 may be regarded as characteristic of the Atlantic coast region, 83 of the region of the Gulf of Mexico, 92 of the southwest, including the states of Texas, New Mexico, Arizona, and southern California, 74 of the states of California, Oregon, and Washington, and 61 of the Rocky mountain region, of which 19 may be regarded as more properly the prairie species of that region." This series will certainly prove very useful in the identification of grasses, a family usually left to the expert.

Bulletin 21 of the same division contains a revision of the North American species of *Chætochloa*, by F. Lamson-Scribner and Elmer D. Merrill. In our older manuals the name was *Setaria*, and the three or four introduced species are very familiar. The name Setaria being untenable, the plants were called *Chamæraphis* Kuntze, not R. Br., and then *Ixophorus* Nash, not Schlecht, and now *Chætochloa* Scribner. In North America there are twenty-eight species of the genus, six of them being described as new in this bulletin. There are twenty-three natives, and of the five introduced European species three are cosmopolitan weeds.— J. M. C.

THE two previous fascicles of the *Flora of the West Indies*[6] have already been noticed in this journal. The third fascicle, just published, completes the first volume, making a book of 536 pages, and contains the following papers; Botanical bibliography of the West Indies, by Urban; Araliaceæ, by Urban; Polygonaceæ, by Lindau; Asclepiadaceæ, by Schlechter; new species, especially Porto Rican, by Urban; Eriocaulaceæ, by Ruhland; Juncaceæ, by Buchenau; and Sabiaceæ, by Urban. Some conception of the unworked condition of the West Indian flora may be gained from the fact that Urban's paper on the new species (especially Porto Rican) occupies over 190 pages. *Syngonanthus* is a new genus of Eriocaulaceæ, containing three species formerly referred to Pæpalanthus.

The first fascicle of the second volume contains a supplementary paper (7 pp.) by Urban upon the botanical bibliography of the West Indies, twenty-seven titles being added. The rest of the fascicle (153 pp.) contains the Cyperaceæ, by C. B. Clarke, twenty-four of the twenty-six genera being presented. The large genera are Rhynchospora (56 spp.), Scleria (30 spp.), Cyperus (27 spp.), Eleocharis (27 spp.), and Mariscus (21 spp.), the great genus Carex being represented by only six species.— J. M. C.

[6] URBAN, IGNATIUS: Symbolæ Antillanæ seu fundamenta floræ Indiæ occidentalis. Vol. I. fasc. III, pp. 385–536; Vol. II. fasc. I. pp. 1–160. Berlin: Gebruder Borntræger. 1900.

A NOTABLE PAPER in the forthcoming 19th annual report of the U. S. Geological Survey is that by Professor Lester F. Ward upon "The Cretaceous formation of the Black Hills as indicated by the fossil plants," with the collaboration of Walter P. Jenney, Wm. M. Fontaine, and F. H. Knowlton. The paper contains 192 pages of text and 116 plates, those illustrating the species of Cycadeoidea (101 in number) being fine half tones. The plants are considered under four heads: (1) fossil cycadean trunks, (2) fossil forests, (3) other Lower Cretaceous plants, and (4) plants from the Dakota group. The surprising development of cycads in the region of the Black Hills is the subject of special interest to botanists. In 1894 Professor Ward described the seven cycadean species then known from Maryland, but the present paper contains the descriptions of twenty-two species from the Black Hills. These American forms all belong to the genus Cycadeoidea (really identical with Bennettites), which is not now regarded as a true cycad, but as forming a distinct gymnosperm group, Bennettitales, coordinate with Cycadales, etc. The whole paper is full of material for the botanist interested in the history or phylogeny of plant groups.— J. M. C.

FOLLOWING the discovery of the numerous gigantic species of Cycadeoidea (Bennettitales) from the Cretaceous of the Black Hills, described by Professor Ward in the 19th annual report of the U. S. Geological Survey, there comes an account of a rich discovery of cycads in the Jurassic of Wyoming (Carbon county). The forms are small and bulbous, and are thought by Professor Ward to constitute a new genus, which he calls *Cycadella*, and under which he describes no less than twenty species. The great feature of the genus seems to be a peculiar outer covering which completely invests and cuts off from view the usual cycadean armor. The statement is that "Cycadella developed an exuberant growth of fine scales or hairs from the bases of its old petioles below the apex, which formed a woolly or mossy covering of considerable thickness, sufficient when tightly appressed to the trunk and petrified there to form a layer 5–15^{mm} thick all over the fossil trunks." The paper appears in Proc. Washington Acad. Sci. 1: 253–300. 1900, and is illustrated by eight half tone plates.— J. M. C.

ALMOST a century ago (1806–1813) Sibthorp and Smith published their *Florae Graecae Prodromus*, and in his *Flora Orientalis* Boissier made such additions as exploration of certain minor regions made necessary. In fact, our knowledge of the Grecian flora has been very incomplete. To supply this lack Wilhelm Engelmann has undertaken the publication of a complete flora of Greece by Dr. E. de Halácsy,[7] than whom no one is more competent, as he possesses abundant material, has traversed the country a number of

[7] HALÁCSY, E. DE: Conspectus Floræ Graecæ. Vol. 1. Fasc. 1. pp. 1–224. Leipzig: Wilhelm Engelmann. 1900. *M* 5.

times, and has already published a number of memoirs upon the subject. The *Conspectus* will be entirely in Latin, and will enumerate with full description, synonymy, and habitat, all the plants of political Greece, with its isles, and also of Epirus and Crete. The work will appear in eight to ten fascicles, each containing about 160 pages, and will be completed in five or six years. The cost of the whole work will not exceed 30 marks, or 38 francs. The preface, bibliography, and keys will appear with the last fascicle. The first one includes Ranunculaceæ to Alsinaceæ, and the sequence is that of Bentham and Hooker.—J. M. C.

THE LAST "Contribution from the Gray Herbarium of Harvard University" appears as *Proc. Am. Acad.* **35**: 307–342. 1900, and contains four papers. The first is by J. M. GREENMAN, entitled "New species and varieties of Mexican plants," and contains descriptions of twelve new species.— The second is by B. L. ROBINSON, entitled "Synopsis of the genera Jaegeria and Russelia." The species of Jaegeria have been much confused with Sabazia, Galinsoga, Melampodium, and Spilanthes. Dr. Robinson recognizes nine species, two of which are new. The genus Russelia contains thirteen species, two of which are new.— The third paper is by E. B. ULINE, entitled "New Dioscoreas from Mexico," and contains descriptions of two species and a new variety.— The fourth paper is by B. L. ROBINSON, entitled "New phanerogams, chiefly Gamopetalae, from Mexico and Central America," and deals chiefly with new species (twenty in number) and specific reductions in the genus *Eupatorium*.— J. M. C.

THE fourth fascicle of Engler's work on the genera and families of African plants[8] has just appeared, completing the Combretaceæ. Notices of the preceding fascicles appeared in the BOTANICAL GAZETTE for January 1899 and January 1900. In the third fascicle a synopsis of Combretaceæ and an elaboration of the greatest genus, *Combretum*, were given. In the present fascicle the nine other African genera are presented, by far the largest being *Terminalia*, with 45 species, 22 of which are described as new. The fascicle is a model of completeness and fine presentation, the plates and figures being especially worthy of commendation. The general conclusions in reference to the African Combretaceæ, apart from those littoral species which belong to the mangrove-formation, is that there is very little relation with either tropical America or Madagascar, but that there is a rich development of endemic groups in the various plant-formations of tropical Africa.— J. M. C.

JANET R. PERKINS has published a "Monograph of the genus Mollinedia," being a dissertation for the doctorate at the University of Heidelberg.

[8] ENGLER, A.: Monographien afrikanischer Pflanzen-familien und -Gattungen. IV. Combretaceæ excl. Combretum, bearbeitet von A. Engler and L. Diels. 4to. pp. 44. *pls.* 15. *figs.* 5. **Leipzig: Wm. Engelmann.** *M* 12.

The genus belongs to the Monimiaceæ, and is peculiar to tropical America, with its greatest development in southern Brazil. In 1868, in his monograph of the genus for the *Prodromus*, A. DeCandolle recognized 28 species, two of them being regarded as doubtful. In the present monograph 71 species are presented, 46 of them being described for the first time.— J. M. C.

A REVISION of the North American species of *Euphorbia* § *Tithymalus* has been published by J. B. S. NORTON in the 11th annual report of the Missouri Botanical Garden, illustrated by 42 plates. Thirty-six species are recognized, eight of them introduced from Europe, and one of them new. The section contains about 400 species of the 700 or more that have been described, but is rather poorly represented in America, the greater number being southwestern and xerophytic.— J. M. C.

NOTES FOR STUDENTS.

MR. FRANCIS E. LLOYD is making a vigorous study of the comparative embryology of the Rubiaceæ. His first paper[9] outlines the task before him and discusses the development of *Vaillantia hispida*, one of the Galieæ indigenous to the Mediterranean region, from earliest stages to mature fruit, paying special attention throughout to the matter of nutrition. The chief characteristics of this species are: a multicellular archesporium; a single integument; migration of the megaspore mother cell and development in the micropyle; great development of antipodals for the sake of securing food to the growing embryo-sac, and the development of a suspensor with cells clustered like a "bunch of grapes," which breaks down with the appearance of the cotyledons. There is found an abundant source of food supply and an efficient means of transmitting it during every stage of development, until finally the plant by way of the vascular region deposits a supply of starch and cellulose in the tissues surrounding the mature embryo.—J. E. WEBB.

BARANETZKY, to whom we owe an improved form of the registering auxanometer, describes[10] a new apparatus for recording the periodic curvatures of leaves and stems. The registering apparatus itself consists of a drum, carrying smoked paper, and rotated by clockwork once in twenty four hours. The writing point, a bit of flexible metal, is attached to a vertical belt, longer than the drum, passing over pulleys actuated in opposite directions by one or the other of two electromagnets on the base. The leaf stalk or stem to be studied is fastened to a swinging lever which actuates a train of three wheels by which the movements are magnified. The third axle carries a spur wheel, which, by bending aside a flexible platinum strip,

[9] LLOYD, F. E.: The comparative embryology of the Rubiaceæ. Bull. Torr. Bot. Club 8: 1–25. *pl. 1–3*. 1899.

[10] Berichte d. deutsch. bot. Gesells. 17: 190. 1899.

closes an electric circuit through one or the other of the electromagnets. One electromagnet, actuating one of the pulleys over which the belt passes, raises the writing point, while the other lowers it, thus recording a corresponding deflection of the organ. In the instrument used by Baranetzky a deflection of 1° was recorded by a 2 mm step in the record line. He thinks the instrument capable of twice as great sensitiveness.—C. R. B.

HOFMEISTER in his description of the Balanophoraceæ, which reappears in the text-books,[11] describes the pistil as a carpel containing a single integumented ovule, attached laterally near the top; fertilization attends the introduction of a pollen tube; a five to eight-celled embryo develops and is attached to the wall of the sac by a suspensor. After a cursory examination of *Balanophora Indica*, using material secured from India, van Tieghem[12] declares that there is no ovule or placenta; that the megaspore is plunged into the tissue at the base of the style; that there is no fusion of polar nuclei, and that fertilization occurs rather indifferently at either the sexual or the antipodal end of the sac. Treub[13] has now published a very close series of figures from earliest stages to mature fruit, drawn from sections of *B. elongata* which occurs abundantly in the neighborhood of the Buitenzorg Gardens in Java. Treub finds no ovule or placenta; there is an epidermal growth above the embryo-sac designated as the style; the polar nuclei do not fuse and the development of the endosperm invariably results from growth and division of the polar cell of the egg apparatus. Periclinal walls cut off a cell in the midst of the endosperm which develops into a five to ten-celled pseudo-embryo. Treub decides against fertilization, but in a species in which staminate flowers occur. Dr. Lotsy,[14] however, confirms him in every particular, including non-fertilization, from observations upon *B. globosa*, a species which, in his neighborhood at least, has no staminate flowers. He objects to using the word "style" at all in comparing this curious organ with the floral structures of other plants. For hints with regard to the course of reduction and its point of departure both Treub and Lotsy look forward to the study of *Rhopalocnemis phalloides* Jungh. and other forms. Dr. Lotsy is very anxious that *Balanophora Indica* be worked over again with much care, and perhaps with special reference to cytological problems.—J. E. WEBB.

[11] ENGLER and PRANTL: Natürlichen Pflanzenfamilien III. 1:261. SCHENK: Handbuch 3¹: 369.

[12] VAN TIEGHEM, PH.: Sur l'organisation florale des Balanophoracées. Bull. Bot. Soc. de France 43: —. 1896.

[13] TREUB, MELCHOIR: L'organe femelle et l'apogamie du *Balanophora elongata*. Bl. Ann. Jard. Buitenz. 15: 1–22, *pl. 1–8*.

[14] LOTSY, DR. J. P.: *Balanophora globosa* Jungh. Ann. Jard. Buitenz. II. 1: 174–186, *pl. 26–29*. 1899.

AN UNUSUAL paper has appeared on *Drosera rotundifolia*. It is a cytological and physiological study of this interesting plant by Otto Rosenberg[15] of Stockholm, whose investigations were conducted chiefly at Bonn. The examination is suggestive of methods of study in cytology that are soon likely to come to the front, namely, studies upon protoplasm that has been subjected to various conditions in the attempt to analyze the factors that influence its minute structure.

The paper is divided into two parts: the first, on forms of nuclear division, and the second, on the physiological behavior of the nucleus. The first part considers mitoses in various tissues, reproductive and vegetative. One notes that the spindles in vegetative cells are developed from caps of kinoplasm, and in the pollen mother cell the presence of a delicate zone of granular kinoplasm and fibrillæ encircling the nucleus indicates the beginning of the achromatic part of the nuclear figure. However, the account of karyokinesis in the pollen mother cell is not sufficiently detailed to offer evidence on disputed points; it appears that the nucleus is small and not altogether satisfactory for such a study.

Of the physiological studies upon the nucleus the most interesting are naturally those on the cells in the tentacles of the leaf. The most fruitful studies consisted of an examination and comparison of certain epidermal cells before and at successive intervals after the leaves had been fed with various substances. These experiments were tried with a variety of foods, such as albumen, peptone, meat, cheese, sugar, bread, hæmoglobin, and other organic substances, and with such inorganic salts as borax, calcium nitrate, calcium phosphate, and ammonium oxalate.

. Feeding the leaves with organic material brings about very shortly changes in the cytoplasm and nucleus in the epidermal cells of the tentacles. Peculiar granules appear in the cytoplasm near the nucleus, and the tannin vacuoles become more prominent. But the most conspicuous effects are exhibited in the nucleus. The chromatin increases greatly in quantity along the linin network, and finally collects as longer or shorter rods on the membrane. Finally, when the reactions are most energetic, the chromatin takes the form of a thick thread and the linin network cannot be followed. The nucleolus during this process of feeding usually grows smaller and smaller until it is very insignificant. But there is no fixed relation between the decrease in the size of the nucleolus and the great increase in the amount of chromatin.

These reactions affect other cells in the tentacle, those of the endodermis and stalk exhibiting similar changes.

In general one may say that the feeding of a leaf almost always results in

[15] ROSENBERG, O.: Physiologisch-cytologische Untersuchungen über *Drosera rotundifolia* L. Upsala 1899.

the excretion from the epidermis of slime, and this is accompanied by decrease in the amount of cytoplasm and usually by a great increase in the chromatin, while the nucleolus becomes smaller. The investigations point to the nucleus as the chief center in the cell, initiating and carrying out the complex chemical and physical reactions.

There is much detail in this paper of 116 pages and apparently a very complete summary of the literature, together with much suggestive speculation interesting to the student of the plant cell.—B. M. DAVIS.

ITEMS OF TAXONOMIC interest are as follows: A. W. EVANS (Bull. Torr. Bot. Club **27**: 97–104. 1900) has described a new genus of Hepaticae (*Acromastigum*) from the Hawaiian islands, heretofore referred with doubt to Mastigobryum (Bazzania). —E. L. MORRIS (*ibid.* 105 119) has published a revision of the species of Plantago commonly referred to *P. Patagonica* Jacq., in which fifteen species are recognized, six of them being described as new.—E. B. ULINE (Field Columbian Mus. Bot. Series **1**: 413–422. *pls. 22–24.* 1899) has described a new genus (*Higinbothamia*) of Dioscoreaceæ from Yucatan, a new Dioscorea, and five new species of Amaranthaceæ.—In the current number of Engler's *Botanische Jahrbücher* (**28**: 145–272. 1900) the present series of papers (XIX) on the African flora is completed. E. GILG describes a new genus (*Brachythalamus*) of Thymelæaceæ; E. GILG and K. SCHUMANN describe a new genus (*Maschalocephalus*) of Rapateaceæ; TH. LOESENER publishes his third paper on African Celastraceæ; F. KRÄNZLIN presents the African Orchidaceæ, describing two new genera (*Angraecopsis* and *Schwartzkopffia.*) In the same number P. HENNINGS publishes a list of Japanese fungi, describing a new genus (*Hydnofomes*) of Hydnaceæ.— In *Deutsch Bot. Monats.* (**18**: 26–27. 1900) W. N. SUKSDORF publishes three new species of Saxifraga, and a new variety of *Vicia Americana*, all from Washington.—J. M. C.

NEWS.

DR. HERMAN AMBRONN, of Leipzig, has been called to a professorship in the University of Leipzig.

THE French Academy of Sciences has elected as corresponding members in the section of botany Professors Schwendener and Pfeffer, in place of Baron Müller and Professor Cohn, deceased.

PROFESSOR A. S. HITCHCOCK, of Kansas Agricultural College, has been elected director of the *Académie internationale de géographie botanique* for 1900, succeeding Casimir DeCandolle. A portrait is published in the *Bulletin* for March.

M. ADRIEN FRANCHET died suddenly on February 15 in his sixty-sixth year. He is best known as the author of the *Flore de Loire-et-Cher*, monographs of Verbascum and Strophanthus, the *Flore du Japon*, the *Plantae Davidianae*, the latter the elaboration of the collections of the abbé David in Mongolia and eastern Thibet, and the *Sertum Somalense*.

AT THE meeting of the Academy of Science of St. Louis on March 19, 1900, Mr. H. von Schrenk exhibited some burls on the white spruce (*Picea Canadensis*). The burls, unlike most of those so far known, are almost round, and are covered with smooth bark. They grow of various sizes, and occur on the trunk and branches of a group of spruces limited to a small area. The wood fibers are arranged in annual rings; they differ from normal wood fibers because of their thinner walls and greater internal diameter, giving the wood a spongy character. Long rows of secondary resin passages occur in each ring. The largest burls, which are from one to three feet in diameter, have rows of long holes within each ring. These holes are diamond-shaped in cross-section, the longer diameter extending radially. Between the holes the wood fibers are compressed tangentially. The speaker explained that the holes must have resulted from an excessive radial pressure exerted from without, probably by the bark. No holes were found where the bark pressure had been released, *i. e.*, where the bark had burst. These results are not in harmony with the findings as to bark pressure reached by Krabbe. The speaker described the manner in which burls are usually formed, and showed the way in which these burls form, by excessive growth, induced by a wound or branch stump.—WILLIAM TRELEASE, *Secretary*.

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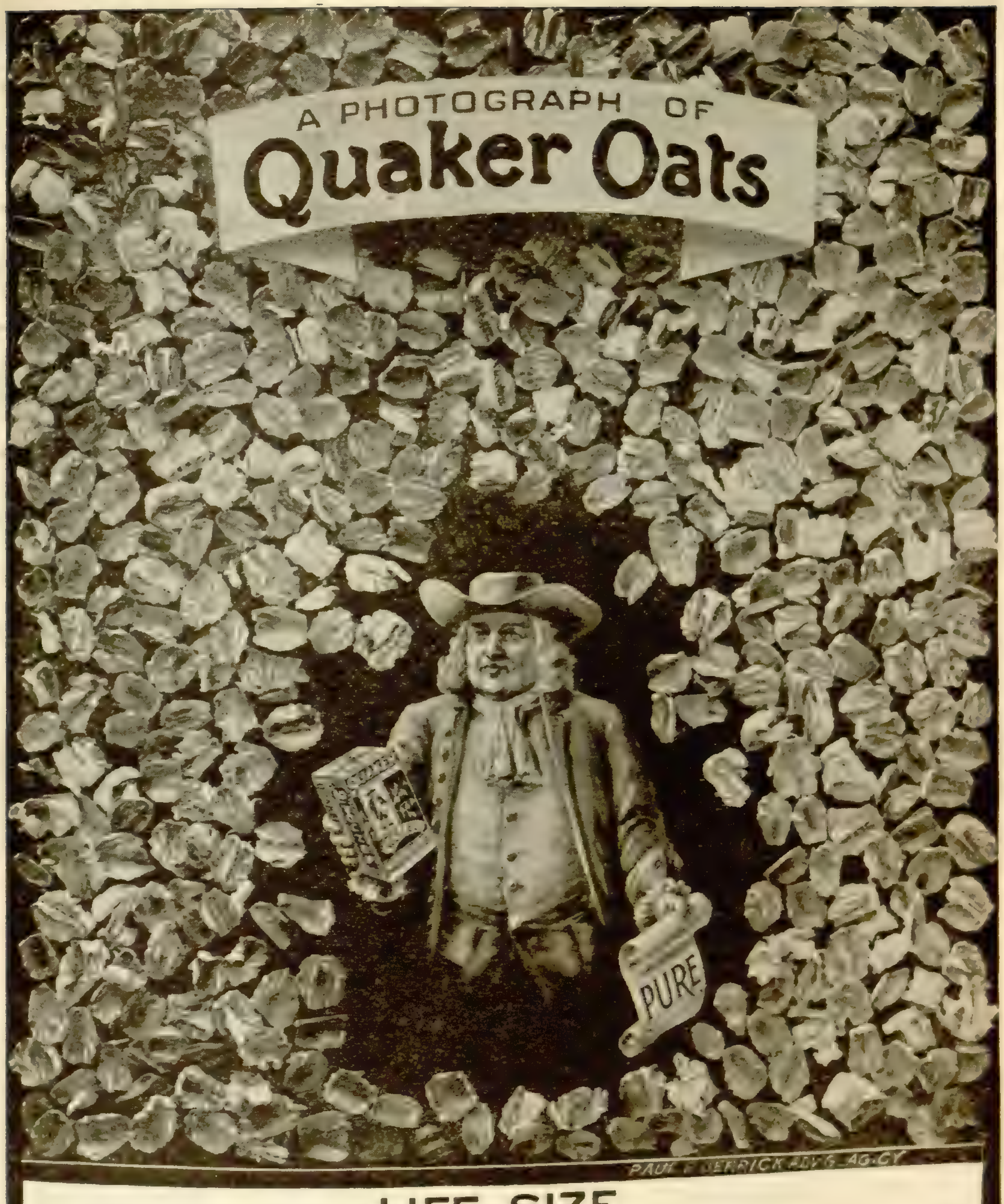

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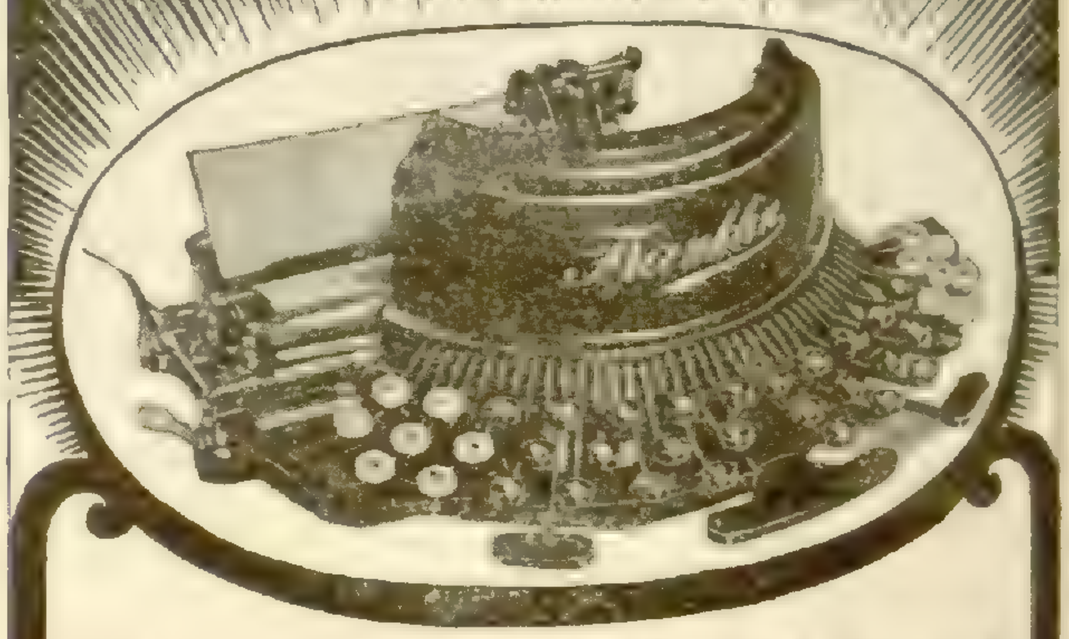

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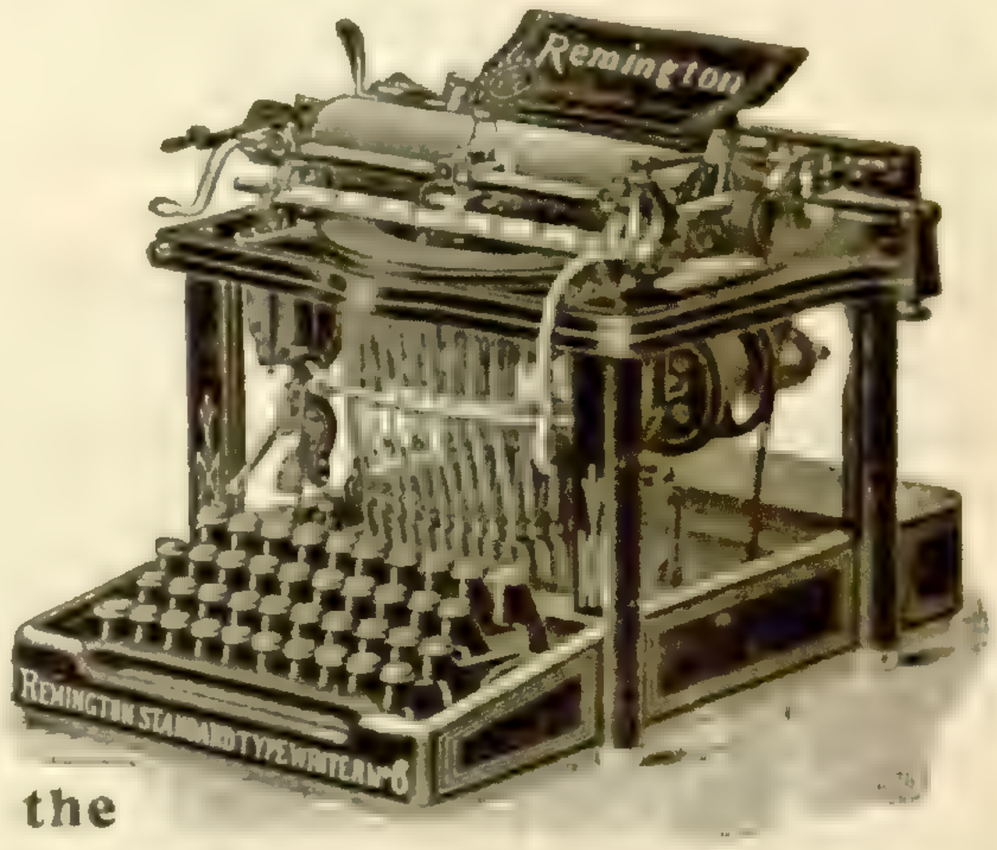

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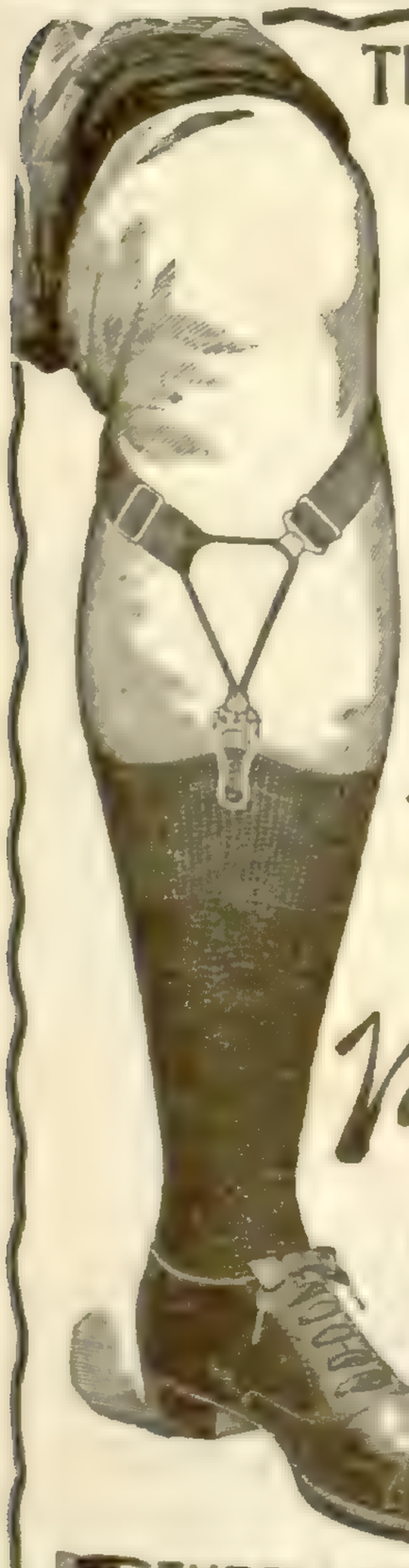

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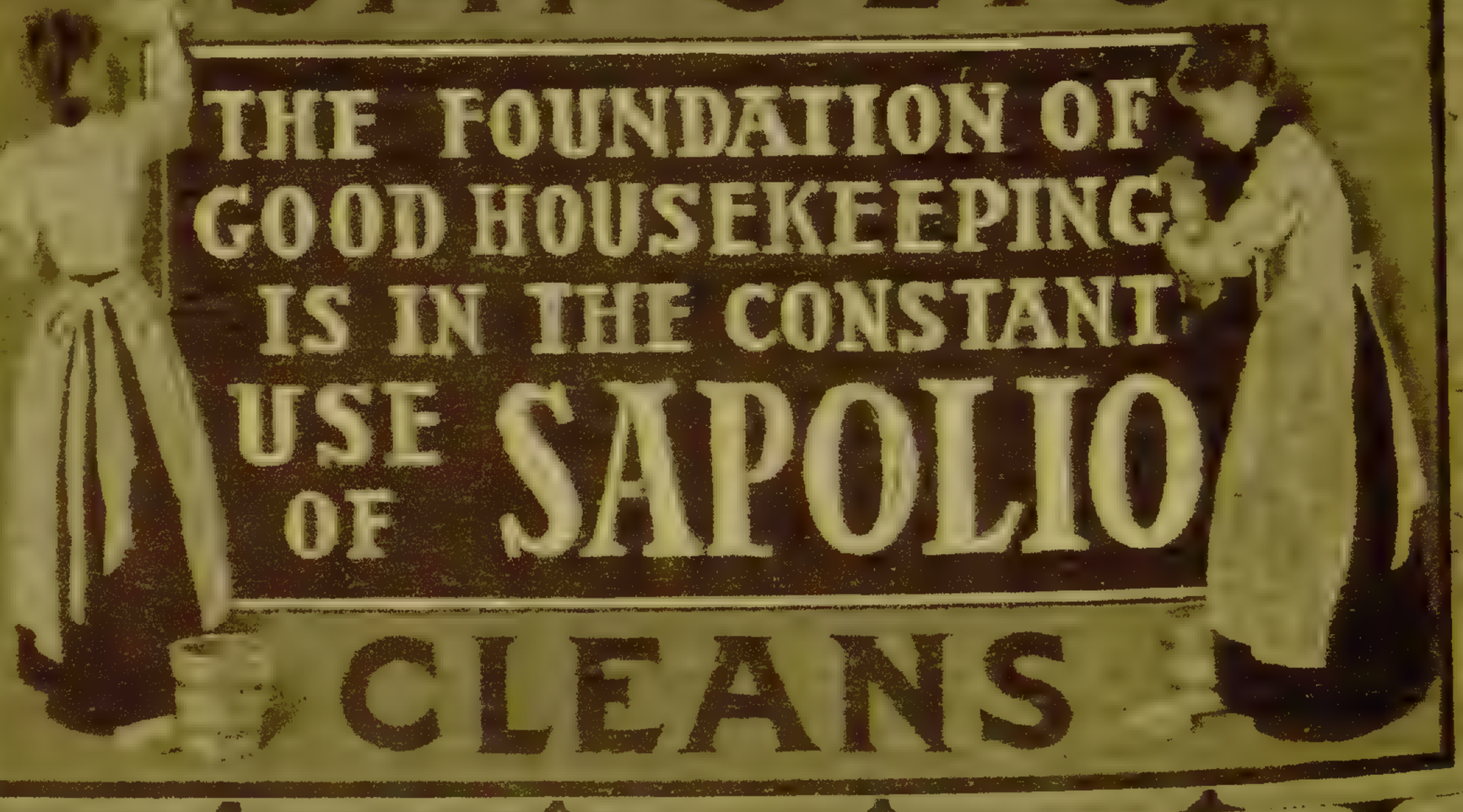

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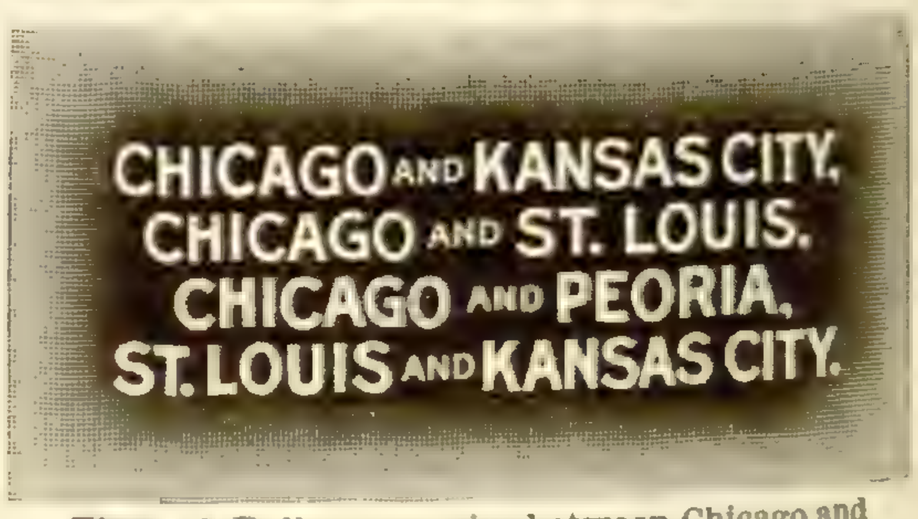

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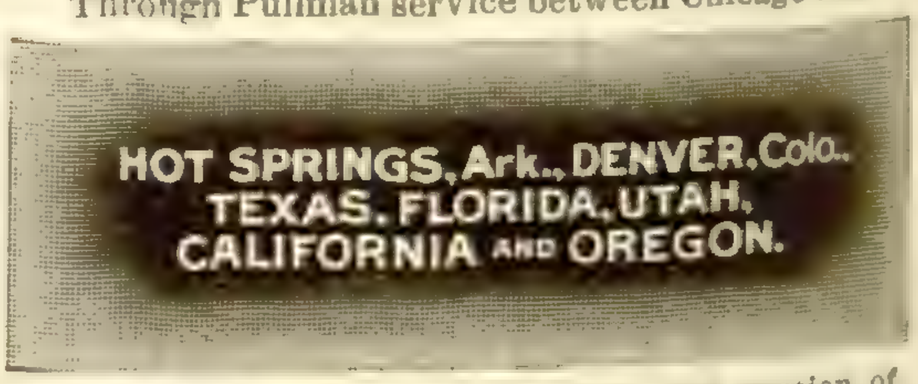

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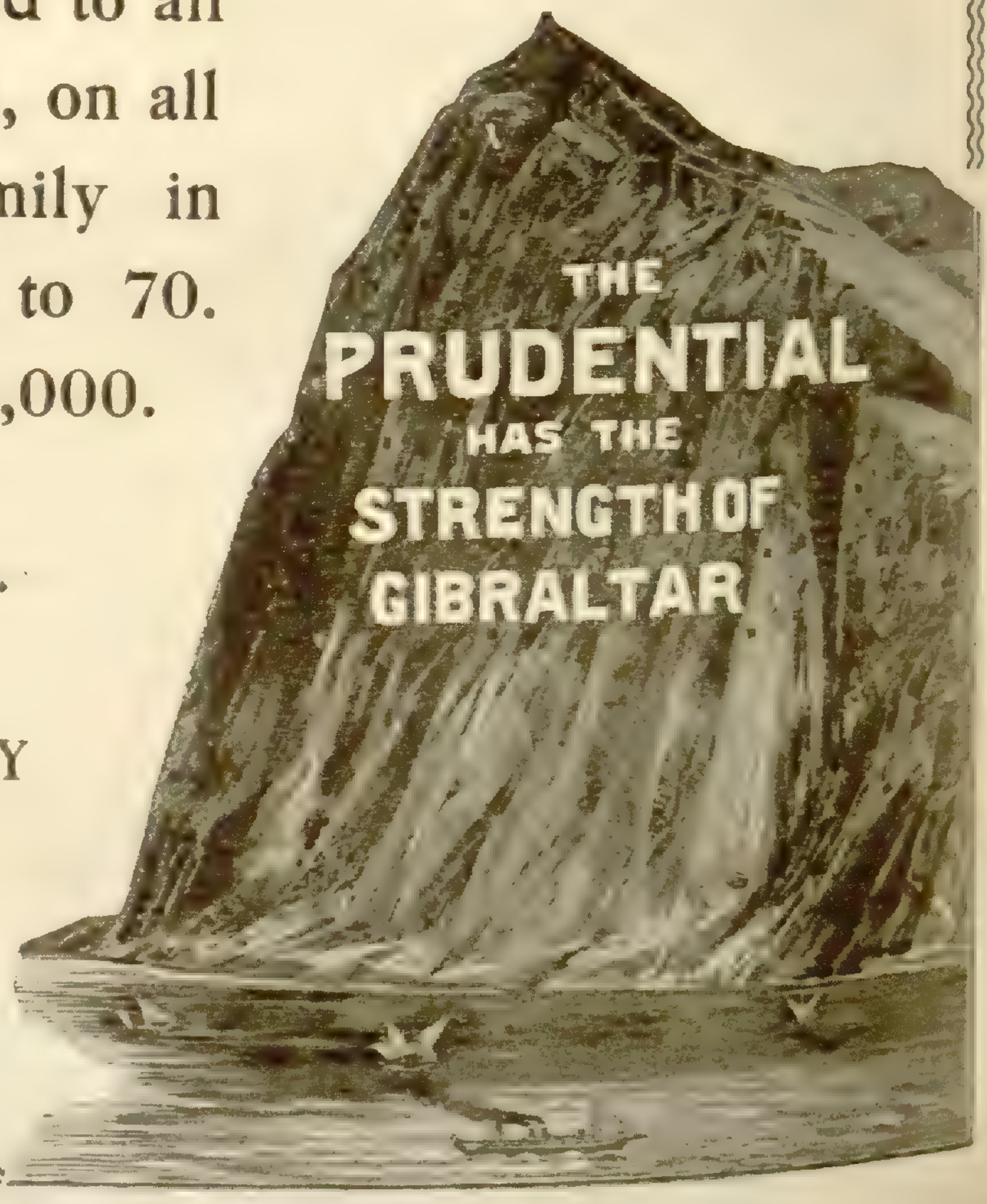

VOLUME XXIX NUMBER 5

BOTANICAL GAZETTE

MAY, 1900

THE FERTILIZATION OF ALBUGO CANDIDA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XIX.

BRADLEY MOORE DAVIS.

(WITH PLATE XXII)

THE recent studies of Mr. Stevens (99) upon *Albugo bliti* have yielded some exceedingly interesting results, which are very suggestive when considered and applied theoretically to a number of the Phycomycetes whose sexual processess are so little understood. Indeed, it is possible that the generally accepted views as to the homologies of sexual organs in certain members of this group may be materially changed with the newer standpoint.

It was my privilege to follow the investigation of Mr. Stevens throughout its progress. Many questions arose for future investigation to test the suggestive conditions presented by *Albugo bliti* in other Phycomycetes. It seemed also desirable to re-examine related species of Albugo, and Mr. Stevens very kindly gave me his collections of the oft-studied *A. candida*, which furnished the material for this study.

The results confirm the views of the earlier investigators, Wager (96) and Berlese (98), as to the behavior of the sexual nuclei. But a somewhat more detailed examination of a number of points in the cytology of the oogonium will, I trust, warrant the publication of this paper. The writer has also allowed

himself to discuss the subject of fertilization in which multinucleate gametes are concerned, endeavoring to present a point of view that seems to him fruitful of future results. This portion of the paper is headed Theoretical Considerations.

The material of *A. candida* came from the vicinity of Columbus, Ohio, and had been fixed by three methods, in chrom-acetic acid, by the weak formula of Flemming, and in saturated solution of corrosive sublimate. That fixed in chrom-acetic acid proved very much the best for the present study, which desired the protoplasmic contents of the cells as free as possible from all inclusions such as oils and fats. It is interesting to know that the osmic acid of Flemming's fluid so preserved the oil-like material in the protoplasm as to render it insoluble in ordinary clearing agents, and very troublesome in all preparations, because the globules stained deeply and masked the protoplasmic elements. The material killed in corrosive sublimate did not present well-preserved nuclei or mitotic figures. The sections, cut 5μ thick, were stained with safranin, gentian-violet, and orange G.

The preparations confirmed in all essentials Wager's account of the development of the oogonium and antheridium.

A most interesting stage in this process is the differentiation of the so-called "receptive spot," a region of densely staining protoplasm in the oogonium at the point where the antheridium becomes applied to the structure. It is certainly true that a papilla from the oogonium is the active agent which works its way through the cellulose walls and establishes communication with the antheridium. In *Albugo bliti* the papilla actually pushes into the antheridium, becoming a swollen process in the interior of that structure. The papilla is much less pronounced in *A. candida*, but behaves in a strictly analogous fashion.

The antheridial tube begins its development and growth into the oogonium before there is the slighest trace of the oosphere, and it may have penetrated to one fifth the diameter of the structure before that cell is differentiated.

The development of the oosphere is an exceedingly interesting and complex process. Its commencement is indicated by a

gradual accumulation of the protoplasm at the center of the oogonium. The nuclei, very variable in number (Wager estimates from 70–110), are at first in the resting condition, but very soon prepare for and pass through a mitosis. They lie in a coarsely vacuolate cytoplasm.

The first stage in the differentiation of the oosphere is illustrated in *fig.* 1, which shows a slight but not conspicuous increase in the granular protoplasm at the center of the oogonium. There soon appears, however, a remarkable structure in this region of denser protoplasm. It develops form and organization, and finally becomes a very prominent element in the oogonium. Mr. Stevens found a similar body in *A. bliti*, appearing at this period in ontogeny, and believing it to be associated with important activities in the oogonium called it the "coenocentrum."

The coenocentrum of *A. candida* is very much larger than that of *A. bliti*, and has attracted the attention of several observers. Wager was the first to recognize its protoplasmic nature, which appears unquestionable through its structure, development, and reaction to stains and clearing agents. When fully differentiated the coenocentrum is a sphere of dense, deeply-staining, slightly granular protoplasm, entirely free from inclusions, and two to four times the diameter of the nuclei. It is sometimes surrounded by a zone of lightly staining protoplasm, as is shown in *fig.* 2, through which delicate radiations may be traced. The coenocentrum develops, as has been said, from an accumulation of protoplasm in the center of the oogonium (*fig.* 1). It reaches its most beautiful state of differentiation when the appearance is that presented by *fig.* 2. Later the structure contracts somewhat, rounds itself off, and becomes a very dense body with a firm outline, as is indicated in *figs.* 3–6. It is then very conspicuous, staining deeply, but is not so plainly related to the cytoplasm as in earlier stages. Certain investigators have mistaken these later conditions for accumulations of oil or similar matter.

The differentiation of the oosphere, that is the separation of the ooplasm from the surrounding periplasm, is heralded by the

appearance of the coenocentrum. The phenomenon is remarkable. It consists of an inward movement of the protoplasm toward the center of the oogonium, and a consequent floating out of the larger vacuoles to the periphery. The position of the nuclei is also affected so that they pass from the interior to variable distances between the coenocentrum and the wall of the oogonium. At a certain stage the nuclei may be found in a hollow sphere of protoplasm, at or just outside of the position where the wall of the oospore will finally be laid down. This is the very interesting and striking condition to which Mr. Stevens has applied the term "zonation."

Zonation is a very prominent stage of oogenesis in *A. candida*, although not as conspicuous as in *A. bliti*. It is similar in all important particulars, as may be seen by comparing *fig. 2* of this paper with *figs. 61, 62, 64, 65* of Mr. Stevens' article. The agreement is made more striking by the fact that in *A. candida* also the nuclei are usually in mitosis at this time. At the completion of zonation the ooplasm may be said to be differentiated from the periplasm, and only lacks the necessary female sexual nucleus to become the oosphere ready for fertilization.

At this point in oogenesis *A. candida* and *A. bliti* depart widely from one another. The oosphere of *A. candida* is uninucleate. One of the nuclei from a point near the periphery of the ooplasm slips back to the center and takes a position near the coenocentrum (*figs. 3, 4, 5*). One may find stages where such a solitary nucleus lies midway between the coenocentrum and the periplasm, but it is exceedingly difficult to determine in such cases whether the nucleus is returning to the center of the ooplasm or passing to the exterior. In the former case it would always be a resting nucleus, in the latter it might be in mitosis.

There can be no question but that the oosphere of *A. candida* is quite generally if not universally uninucleate. There are theoretical reasons why in the light of Mr. Steven's results with *A. bliti* one may expect some variation in this particular, and that *A. candida* may at least occasionally have a multinucleate

oosphere. Indeed a few of the author's preparations look suspicious, but their rarity would make the establishment of such a point a very tiresome and laborious investigation, if possible at all.

It will be remembered that in *A. bliti* (according to Stevens' paper) a large number of nuclei pass into the ooplasm when the oosphere is differentiated, and these are doubled in number by a mitosis, so that the oosphere when ready for fertilization contains about one hundred nuclei, and may be described as a compound oosphere. Fertilization is effected by the introduction of a large number of sperm nuclei (about one hundred) from the antheridial tube, and these, after becoming distributed through the ooplasm, finally fuse in pairs with the female nuclei.

It is very surprising that two species of the same genus, organisms so closely related as are *A. candida* and *A. bliti*, should present such a remarkable distinction as regards processes of fertilization. It was this that led the author to the examination here described. But *A. candida* certainly presents, as all investigators agree, the characteristics of the usual method of fertilization, when one male nucleus fuses with one female in an oosphere. If there is any variation in this particular it has not been demonstrated, and is probably very rare, although theoretically possible. It is to be hoped that some material of this or other species will be found to bridge over the gap between the conditions illustrated by *A. candida* and *A. bliti*.

Passing on for the present to the consideration of the antheridial tube, there is nothing to be said except in confirmation of previously published accounts. The tube at the time of zonation (*fig. 2*) is very near if not directly applied to the ooplasm. It rapidly elongates and increases in size until there is presented the club-shaped structure shown in *fig. 3*, containing granular protoplasm. A nucleus, the sperm, very soon slips from the antheridium and occupies a position in the dense cytoplasm near the tip of the tube, as is shown in *figs. 3* and *4*. The delicate wall around the tip of the antheridium finally dissolves, and the sperm nucleus is introduced into the ooplasm, at first surrounded

by a quantity of granular cytoplasm from the antheridium (*fig. 5*), which immediately mingles with that of the oogonium.

Although there is no proof that more than one sperm nucleus ever enters the oosphere, it is well to note that other nuclei may be present in the upper portion of the antheridial tube. Such an example is shown in *fig. 3*, where one perfectly organized nucleus occupies the neck of the tube. It would not seem strange to the writer if material were sometimes found where several nuclei occasionally or frequently occupied the tip of the antheridial tube, and were introduced into the ooplasm at the time of fertilization.

The sperm nucleus begins to move towards the center of the oosphere, and finally fuses with the female nucleus near if not actually adjacent to the coenocentrum. *Figs. 6* and *7* show the two sexual nuclei close to one another, and *fig. 8* is of a fusion nucleus.

An important change usually comes over the coenocentrum before or during the fusion of the sexual nuclei. The body so clearly differentiated at the time when the antheridial tube first enters the ooplasm becomes less and less clearly defined, and at last completely disappears.

The dissolution of the coenocentrum may be accomplished in two ways. The structure may increase in size, the outline becoming vague, until there is finally present an irregular mass of protoplasm usually surrounding the fusion nucleus. Or the coenocentrum may fragment into several portions, as is shown in *fig. 7*, and these later swell and merge into an unorganized granular protoplasmic mass.

It seems quite certain that the coenocentrum is not a permanent structure in the protoplasm. Arising as an accumulation of protoplasm at the center of the oogonium, the coenocentrum becomes most pronounced when the oosphere is organized, but finally all trace of the body is lost in the ripening oospore.

The suggestion of Swingle (98) that the coenocentrum is an organ of the oosphere seems less probable when we consider its temporary character. Yet it is possible that the coenocentrum

may have important functions to perform during oogenesis. The differentiation of the ooplasm and the separation of the female nucleus from all the other nuclei of the oogonium which pass into the periplasm is a remarkable phenomenon. However, there is little or no evidence furnished by morphology as to the part which the coenocentrum might play in these activities. On the other hand, there is the possibility that the structure may represent only an effect of functions concerned with the protoplasm of the oogonium as a whole. It may be the morphological expression of dynamic activities deeply seated in the protoplasm, such as might be presumed to operate when the ooplasm collects in the center of the oogonium, when the nuclei pass outward into the periplasm, and when the female nucleus is chosen to preside over the oosphere. This point of view is worth considering, although we have not yet enough data to safely advance such a theory.

The nuclei of *A. candida* are so small that the study of the mitotic figure is very difficult. Stages of division are always numerous in preparations, because both the antheridium and oogonium present a mitosis at one stage of their development, apparently affecting all of the nuclei simultaneously. The mitosis in the oogonium takes place when the ooplasm is differentiated from the periplasm; that in the antheridium before the penetrating tube has entered the ooplasm. Metaphase is a very conspicuous stage. As is shown in *fig. 10* the spindle is entirely intranuclear. The writer was not able to establish with certainty the presence of centrosomes, but the nuclear figure is very small, and proportionally a centrosome might be expected to be exceedingly minute. The chromosomes are granular, and the number can only be estimated with great difficulty, but Wager's view that there are about 12 or 16 is probably correct. They arise from a linin network that may be readily stained in the resting nucleus (*fig. 9*). The nuclear membrane persists until late anaphase, as is illustrated in *fig. 11*, where the two sets of daughter chromosomes are shown separated and massed at the poles of the elongated nucleus. The old nuclear membrane

finally dissolves, leaving the two groups of daughter chromosomes quite apart (*fig.* 12), after which each daughter nucleus proceeds to organize its new membrane. The intervening space, at first vacuolate, becomes filled with granular cytoplasm and the mitosis is finished.

There appears to be no positive evidence that the mitoses described above for the oogonium and antheridium are reducing divisions, whatever may be the speculations upon that point. Little can be said on this subject in our present very incomplete knowledge of the mitotic figures at other periods in the life history of Albugo. The study of the oospore may lead to some important results, although the writer's incomplete observations were no more promising than the examinations of Wager (96), Berlese (98), and Stevens (99). An investigation of this subject is much to be desired, and should include the study of the nuclear figure at some period of vegetative activity. *A. candida*, however, is not the most favorable subject for such an examination, as the nuclei are small. *A. portulacae* or *A. bliti* would be more satisfactory.

THEORETICAL CONSIDERATIONS.

The writer must confess a feeling of considerable uncertainty as to the cytological conditions and perhaps homologies of the sexual organs found in certain Phycomycetes. Much interesting material is likely to be presented through future investigations in this field, and particularly upon those forms whose gametes are well known to be multinucleate. Accordingly any review of the present situation can only offer suggestions of what may later become established by research. The subject is a very interesting one, but the difficulties of investigation are unusual, not only on account of the necessary technique, but in the nature of the material that must be studied.

It is well known that the gametes of certain fungi contained in the Mucorales are multinucleate. Several investigators have studied these structures, and the zygospore which results from their fusion, but none have given a clear account of the cytologi-

cal phenomenon exhibited in this act of fertilization. The descriptions of Léger (**95**) and Dangeard and Léger (**94**) present some interesting conditions, which, however, are very difficult to understand in the light of generally accepted theories of fertilization, and certainly are not at present thoroughly explained.

When the term gametes was first applied to the fusing cells that formed the zygospore of a mould, it was probably in the belief that these were sexual elements pure and simple, homologous with other sexual cells, such as the oospheres and sperms of the algæ, the fusing cells in forms of the Conjugatae, or the members of a copulating pair of swarm spores. The term gamete had a strict morphological significance implying general homologies, in most cases very close, in other instances more remote, or possibly only a relationship through some earlier non-sexual form of spore.

At present the gamete probably stands in the minds of most botanists as a morphological unit, with a structure essentially the same in all realms of biology. The gamete is a uninucleate sexual body, with a greater or less amount of cytoplasm which may be very much specialized, as is illustrated in the degree of differentiation shown by the egg and the sperm.

The question that must suggest itself to many is the correctness of the use of the term gamete, with its implied homologies, when designating the fusing sexual elements in a number of Phycomycetes. To state the difficulty concretely: are the multinucleate cells that fuse to form the zygospore of the Mucorales, the antheridial tubes and oospheres of the Peronsporales and Saprolegniales, homologous with the simpler sexual elements of the Monoblepharales and Chytridiales, and the gametes of the algæ? Although we know practically nothing about the cytology of these last two groups of fungi, nevertheless the studies of Thaxter (**95**) on Monoblepharis and the structure of the Chytridiales indicate much simpler conditions than appear in the Mucorales, Peronosporales, and Saprolegniales. They probably agree in all essentials with the sexual processes of the algæ.

In the Mucorales all that we can safely affirm now is the fusion of two multinucleate masses of protoplasm. The history and fate of the nuclei is certainly not clearly understood, but the indications are rather for some complex phenomenon involving many nuclei than a simple act of fertilization, concerned with only two sexual nuclei.

The Peronosporales present two well defined conditions at the time of fertilization. The phenomenon in *A. bliti* is at variance with that established for *A. candida*, and indicated by superficial examination for several other forms. In *A. candida* the sexual act is the fusion of two nuclei, thus satisfying the requirements generally understood by fertilization. In *A. bliti* there are many sexual nuclei fusing in pairs, about 100 sperm nuclei entering a compound oosphere which contains approximately 100 female nuclei.

What are the homologies between these two species? The oogonia and antheridia are certainly homologous structures, and there is no evidence that the nuclei contained within are not likewise. There seems indeed, from the cytological data at hand, good reason to believe that these nuclei are all homologous, both those that fuse and those that remain sexually inactive, either left behind in the antheridium or lying in the periplasm of the oogonium. Our inability at present to distinguish between the various mitoses in either sexual organ offers the strongest evidence of the position above taken. The difference between these two species is perhaps then only one of the number of the nuclei that are actually sexual or gametes in the strictest morphological sense. Nuclei that are not actually sexual, either in the antheridium or periplasm of the oogonium, may stand phylogenetically for a previous condition, when these organs contained a much larger number of sexual nuclei. This point of view seems to have been in the mind of Hartog (91).

The antheridium and oogonium of Albugo are gametangia. However remarkable is the difference between *A. candida* and *A. bliti* it is nevertheless merely a question of the number of nuclei that become sexually functional or active gametes. In

A. bliti there are many such; in *A. candida* the number becomes reduced to two.

Although the oosphere of *Albugo bliti* is in one sense a gamete, we should be careful to note the peculiarities that make such a designation loose and undesirable. In reality, this structure, which was called a compound oosphere by Mr. Stevens (99), is made up of many gametes (sexual nuclei) acting cooperatively in a common mass of cytoplasm. It may appear desirable to some to give a name to such a structure, one that shall express the idea of sexuality, although it may modify the usual conception of a gamete. The writer suggests the term *coenogamete* as applicable to a multinucleate mass of protoplasm, whose individual nuclei are sexual elements.

Let us think of the sexual processes of the mould in this light. The two elements that unite to form the zygospore are multinucleate. It is possible that some or many of these nuclei are sexual in function (this awaits investigation), and if this be true the fusing masses of protoplasm will illustrate admirably the writer's idea of coenogametes. The sexual nuclei are gametes in the strict sense of the word, and the cells that contain them are gametangia.

It seems to the writer that a standpoint is presented which may be of very great service in the investigations that will be necessary to clear up the peculiar difficulties of this field of research. Although the subject must be approached almost entirely theoretically and tentatively, he ventures to suggest some possibilities to await the verdict of future studies.

Is it necessary that the oospheres of the Peronosporales and Saprolegniales be regarded as homologous with similar structures in the algæ? It is conceivable that the degree of differentiation illustrated by the oosphere may have arisen entirely independently of the algæ, after the fungal ancestors of these groups had departed from the chlorophyll-bearing thallophytes.

Let us suppose a group of fungi with gametangia that discharge motile gametes which fuse in pairs in the water after the manner of the swarm spores of many algæ. Such forms might

readily enough have come from several groups of algæ. Let us again suppose such types of fungi to leave the water and live a terrestrial life as parasites or saprophytes. Their gametangia, unable to discharge the gametes into an aqueous medium, and yet required to satisfy the chemotactic influences associated with sexuality, might find the most satisfactory escape from the difficulties of their environment in fusing with one another. In such mingling of the cytoplasm of two gametangia would be presented the possibility of the fusion in pairs of many of the sexual nuclei (gametes) in a protoplasmic medium instead of water. From such conditions might have arisen a zygospore similar to that of the Mucorales.

If a method of zygospore formation should develop in the manner indicated above, what further changes might be expected with the gradual evolution and specialization of the forms? It does not seem unreasonable to suppose that the same tendencies toward the differentiation of sex would appear here as are manifested in all groups of the algæ. It might be advantageous to reduce the number of gametes (sexual nuclei) to provide the functional female ones with a special supply of cytoplasm, and thus to organize one or more oospheres inside a female gametangium. The furthest extreme of such sexual differentiation would be similar to the conditions illustrated by *Albugo candida*, with its single functional female nucleus (gamete), associated with a large supply of cytoplasm (ooplasm). We have in *Albugo bliti* an example of what might be imagined as an earlier stage in such a process of differentiation, for the number of functional sexual nuclei or gametes is large. Nevertheless, the female gametes are collected in a differentiated region of the cytoplasm, the oosphere, and this peculiarity would be a decided advance over the conditions illustrated by the moulds.

It should be noted that the oospores resulting from this differentiation of sex would bear no homologies to analogous structures among the algæ. They would furnish, on the contrary, another illustration of the well established fact that many divergent lines of thallophytes have developed, independently of one another, the oosporic method or sexual reproduction

The bearing of such possibilities as have been considered above upon the phylogeny of the Phycomycetes is of course attractive, but hardly within the range of the present discussion

It may be questioned whether the theoretical consideration of and speculation upon such difficult subjects as these we have so briefly outlined is worth while. Certainly we have few or no facts to warrant the expression of positive opinions, yet attempts to understand clearly and explain even the most obscure subjects may suggest methods of approach to others working for the same ends, and such hopes must be their justification.

SUMMARY.

Communication between the oogonium and antheridium is established by a papilla from the former structure, which works its way through the cellulose walls into the antheridium.

The differentiation of the ooplasm is associated with the appearance of an organized spherical protoplasmic body in the center of the oogonium. This structure has been named the coenocentrum (Stevens, 99).

A conspicuous stage in oogenesis is that called zonation. Then the nuclei, usually in mitosis, lie at or near the inner boundary of the periplasm, and the coenocentrum is very prominent in the center of the ooplasm.

The oosphere is organized after the stage of zonation, when one of the nuclei from near the periphery returns to the interior of the ooplasm, and takes a position close to the coenocentrum. There is one mitosis in the oogonium, which occurs usually at or slightly before the time of zonation. There is no proof that this mitosis is a reducing division. The spindle is intranuclear, and the nuclear membrane persists until late anaphase. It was not possible to establish the presence of centrosomes, possibly because the mitotic figure is very small. The number of chromosomes is probably 12 to 16 (Wager's estimate).

The oosphere of *A. candida* is certainly generally, if not universally, uninucleate. This point was studied with especial care, in view of the conditions described by Mr. Stevens (99) in *A. bliti*.

The tip of the antheridial tube at the time of zonation is very near if not directly applied to the ooplasm. As it penetrates the oosphere a nucleus slips down into the swollen end whose surrounding wall is later dissolved, and the sperm nucleus is then introduced into the ooplasm surrounded by a quantity of dense cytoplasm.

The sperm nucleus approaches the female nucleus and slowly fuses with it in close proximity to the coenocentrum.

The coenocentrum begins to disorganize at about the time of the fusion of the sexual nuclei. The dissolution may be accompanied by fragmentation, but the final result is always the same, namely an irregular ill-defined region of dense protoplasm in the oospore that finally becomes indistinguishable from the surrounding cytoplasm.

The coenocentrum is not a permanent structure in the protoplasm. Arising as an accumulation of cytoplasm, it becomes most conspicuous at about the time of zonation, finally disappearing after the fusion of the sexual nuclei. The writer suggests that it may be merely the morphological expression of the remarkable activities displayed by the protoplasm, of the oogonium as a whole at the time of the differentiation of the oosphere.

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DAVIS on ALBUGO.

EXPLANATION OF PLATE XXII.

The material, fixed in chrom-acetic acid, was cut 5 μ thick and stained on the slide with safranin, gentian-violet, and orange G.

All figures sketched with an Abbé camera under the Zeiss apochromatic objective 2^{mm} ap. 1.30 in combination with compensation oculars.

Figures 1–8 magnified 1000 diameters; 9–12, 2250 diameters.

FIG. 1. Oogonium showing the first trace of the accumulation of the protoplasm in the central region preparatory to the differentiation of the ooplasm; nuclei entering or in stages of mitosis.

FIG. 2. Oogonium at the stage of zonation; nuclei mostly in metaphase and near the inner boundary of the periplasm; coenocentrum very large and surrounded by a zone of lightly staining cytoplasm; antheridial tube penetrating the periplasm.

FIG. 3. Oosphere differentiated with large deeply stained coenocentrum and smaller female nucleus; antheridial tube in the interior of the ooplasm and about ready to discharge the sperm nucleus; another nucleus in the neck of the tube, near the antheridium.

FIG. 4. Oosphere differentiated; antheridial tube (*a*) in adjacent section; coenocentrum and female nucleus shown in (*b*).

FIG. 5. Antheridium discharging its contents into the oosphere; sperm in a mass of dense cytoplasm; coenocentrum very deeply stained, with female nucleus in close proximity.

FIG. 6. Sexual nuclei fusing in oospore; coenocentrum less conspicuous than in earlier stages.

FIG. 7. Sexual nuclei approaching one another; coenocentrum fragmenting.

FIG. 8. Fusion nucleus; coenocentrum dissolved into an ill-defined region of dense cytoplasm.

FIG. 9. Resting nucleus with prominent nucleolus and delicate linin network.

FIG. 10. Nucleus in metaphase of mitosis; spindle intranuclear.

FIG. 11. Nucleus in anaphase of mitosis: nuclear membrane still persisting.

FIG. 12. Daughter nuclei after mitosis; old nuclear membrane entirely dissolved.

COMPARATIVE STUDY OF THE DEVELOPMENT OF TRICHURUS SPIRALIS AND STYSANUS STEMONITES.

H. HASSELBRING.

(WITH PLATES XXIII AND XXIV)

TRICHURUS SPIRALIS.

DURING the autumn of 1898 a hyphomycete, closely resembling the members of the genus Stysanus, was found on decaying wood brought into the laboratory of Cornell University. The principal difference between this fungus and the species of Stysanus lies in the fact that the capitulum of the former is densely beset with long, tortuous, sterile threads, recalling at first sight the spiral setae surrounding the perithecia of some species of Chaetomium. This character shows the plant to be closely related to *Trichurus cylindricus* Clements & Shear.[1] In the following pages I will refer to it as *Trichurus spiralis*, leaving a discussion of its history and nomenclature until the end of this paper. The plant was obtained in pure culture, and grown on agar and on bean stems, in order to study the development of the sporophore, and to determine, if possible, whether any other forms of fructification existed in the life cycle of the fungus.

The perfect sporophores of *Trichurus spiralis*, growing on agar or on bean stems, appear as small fluffy heads, which are either linear or elongated oblong, and obtuse or pointed at the summit. In agar they appear in small clusters of several heads near the center of the colony, but when grown on bean stems they arise over the entire surface of the substratum. Usually the sporophores are simple, but not infrequently they are branched near the base, and bear several smaller heads, or the head itself may be divided above. These rather abnormal forms are probably caused by an abundance of nutriment. While

[1] Rept. Bot. Surv. Nebraska 4:7. 1896.

fresh and growing the heads are blackish gray, but when dry they assume a copper tint, or rather a color resembling the so-called purple-brown of the dark-spored agarics. The heads are supported on thin black stalks, which are usually longer than the head itself. The entire sporophore varies in length from 0.75 to 2^{mm}; sometimes under favorable conditions larger heads are formed on bean stems, but this would scarcely occur in nature.

The microscopic structure of the sporophore is shown in *fig. 1*. The stipe is made up of many brown septate threads, growing closely together in a strict fascicle. Near their summit the threads send out many short bottle-shaped basidia, which, without being attenuated to a distinct sterigma, bear long chains of spores. Among the spore-chains there arise many long tortuous threads, which form the distinguishing characteristic of this plant. The threads are brown near the base, becoming hyaline at the tips, and give the head the characteristic flocculent appearance. From the base of the stipe numerous threads radiate in all directions. These threads are septate like those of the stipe. They are brown near their origin, but terminate in hyaline growing points. They will be more fully treated below.

The ripe spores of this plant are oval to oblong, with rounded or pointed ends (*fig. 2*). In a single preparation, however, so many variations from this form are found that this description cannot be strictly applied. Sometimes they are even and quite regular in shape; then again one or both ends may be pointed lemon-form; or the entire spore may be more or less inequilateral and irregular. Under the microscope they are dilutely yellowish-brown. The differentiation between the wall and content cannot be recognized easily, the entire spore appearing as a homogenous disk surrounded by a dark refractive ring. With high powers and careful focusing the wall and protoplasm can be made out. The spores are about 5–6 μ in length, by 2.5–3 μ in diameter.

When these spores are sown on agar, germination begins immediately, and the spore swells until it is nearly twice its

original size. At the same time the refractive ring disappears, and the protoplasm becomes distinctly granular and vacuolate. The wall on one side then seems to undergo a change. It becomes thin and delicate, until it can scarcely be distinguished, finally bulging out in the form of a short stout germ tube, whose diameter nearly equals the length of the spore (*fig. 3*). The rest of the spore membrane remains as a sort of cap over the end of the germ-tube. The entire protoplasm of the spore is used in the formation of this first germ tube. The formation of a second similar one would seem impossible, and was never observed. When this primary germ tube has attained a length about equal to the diameter of the spore, it sends out two branches from opposite sides of its broad terminal portion. This formation of a primary tube before the appearance of true hyphae is not unlike the mode of germination of the gonidia of *Completoria complens* by means of a proembryo, as described by Professor Atkinson;[2] or it may be compared to the extrusion of the endospore in *Ceratostoma brevirostre* before the formation of a true mycelium, as described and figured by Miss Nichols.[3] The first mycelial branches are thin, about 3–4 μ in diameter, and elongate rapidly, usually in opposite directions (*fig. 4*). The protoplasm in the older parts of the tubes is rather coarsely granular, with many irregular indistinct vacuoles. Near the growing portion it is homogenous, and at the tips perfectly hyaline. Numerous lateral branches soon arise in a very irregular manner from the main hyphae, being directed at a more or less acute angle to them (*fig. 5*). The branches have the same general appearance as the threads from which they arise, and equal them in diameter, and all hyphae of the mycelium contain numerous septa.

At the end of four days the mycelium has developed a well defined compact colony about 5^{mm} in diameter, with an even margin. The colony consists of a mass of threads so wedged

[2] Damping-off. Cornell Univ. Exp. Sta. Bull. 94 : 233–272. *pls. 6.* 1895.

[3] The morphology and development of certain pyrenomycetous fungi. BOT. GAZ. 22 : 301–328. *pls. 3.* 1896.

in together that they form a thick mat. None of the vegetative hyphae grow above the agar, so that the colony never presents a flocculent appearance.

If at this time one of the colonies is lifted out of the agar and examined under the microscope, its surface will be found to be dotted with small peculiar sporophores, resembling very much the conidial fructification of Penicillium, or still more, perhaps, on account of the slight coloration of the spores, the form genus Haplographium (*figs. 6, 7*). These gonidiophores show great variability. Those first formed consist of a single erect hypha bearing a chain of gonidia at its summit. Others have three or four branches, each with a chain of gonidia. In the older parts of the mycelium, toward the center of the colony, these small gonidiophores become more and more complex (*fig. 7*). Their branches divide and subdivide until it is impossible to represent them. In some of the gonidiophores a sterile branch takes the place of a basidium (*fig. 7*), and later, when the colony is a little older, all the gonidiophores bear long-curved setae, many times longer than the entire fruiting head, so that it sometimes seems as if a small stalk had spent all its effort in producing one of these enormous curved setae.

In these sterile threads, intermingled with the chains of gonidia, one sees a resemblance between the Penicillium form and the perfect sporophores. In time, still greater similarity appears. The heads formed near the center of the colony begin to assume a different appearance. The stalks are considerably elongated, and become brown and septate before the head of gonidia is formed (*figs. 8, 9*). Often two or three grow near together, forming a distinct stipe like that of the perfect sporophore in every respect except size. The stalk hyphae do not remain simple, but send out branches from their lower cells. These branches grow upward and soon attain a diameter equal to that of the stalk. The manner of origin of these branches can be seen best in the more simple sporophores. They are usually sent out from the lower cells, always originating immediately below a septum (*figs. 9, 10 a*). *Fig. 8* shows a small

sporophore which originated from a single erect hypha. The two lower cells have sent out branches, which, together with the original hypha, have formed a stalk bearing a small head of gonidia at its summit. The young branches are hyaline at the tips, but brown in the older portions. They soon become merged with the other hyphae forming the stipe.

In the more complex forms of the small gonidiophores there is seen an approach to the perfect sporophores of Trichurus. In fact, they are identical with the latter both in structure and manner of formation, differing only in the number of hyphae which go to make up the stipe and head. It is easy to form a complete series, showing all gradations from the simplest hypha bearing a single chain of gonidia to the most complex sporophore with several hundred spore-chains.

At a time varying from four to six days after sowing, the vegetative hyphae have formed a dense mat of mycelium in the medium in which they are growing. At the center of the colonies the threads become so numerous and interwoven that they form almost a stroma. From this stroma-like mat the perfect sporophores arise, either singly or in small clusters. They first appear as stout fascicles of hyphae, which arise perpendicular to the substratum. The growing points of the threads are hyaline, but in the older parts of the bundle they assume the characteristic brown color of the stipe (*fig. 18*, of *Stysanus stemonites*).[4] The threads branch in the manner described above, the branches remaining closely appressed to the bundle and growing with it. During longitudinal growth the central threads are in advance of the peripheral hyphae, giving the bundle a linear, pointed form. Before the bundle has completed its growth, the individual hyphae begin to send out small, curved branches or basidia at some distance from their growing points. The basidia are thus formed in centripetal order. Those first formed begin to bear chains of spores before the bundle or stipe has completed

[4] The formation of the stipe and head in the two forms, *Trichurus spiralis* and *Stysanus stemonites*, is exactly alike, and it was not considered necessary to represent this stage more than once. *Figs. 18* and *19* are from Stysanus, but they will answer equally well for Trichurus.

its growth. Finally, the threads themselves cease to elongate, their ends become rounded and enlarged, and begin bearing chains of spores like the basidia (*fig. 19*). Thus the hyphae of the stalk finally terminate in basidia. Septa are formed in the threads of the stipe somewhat later than the basidia, but their formation progresses in the same order, from the base upwards.

The basidia, as has been said, appear as short, curved, rather blunt branches. Like all growing parts they are at first hyaline, and their tips remain colorless throughout. They elongate slightly, resembling a short bottle in shape. The first spore begins to appear at the end of the basidium as a globular swelling which increases in diameter until it has reached the normal size of a mature spore. Before the first spore has completed its growth the tip of the basidium just beneath it enlarges, and a second spore appears below the first. The tip of the basidium continues thus to elongate and to cut off spores until a long chain is formed, or until the nutriment is exhausted. The exact number of gonidia thus formed in a chain cannot be well determined, as they are very much tangled in the head, and when mounted in water they break apart instantly. Sometimes, however, a gonidiophore which has sunk down into the agar is found with some of its chains partially unbroken. In these chains fifteen to eighteen spores were often counted, but the total number is probably much greater. The individual spores are connected by a short isthmus which can be distinguished with difficulty, in the mature chains, but when spores lying on the agar have begun to germinate, it can be distinctly made out as a short tube connecting the swollen spores.

The sterile threads push out from the heads soon after the formation of gonidia has begun. When first seen they are straight, being directed at right angles to the long axis of the head. They are at first hyaline, but as they grow longer they become brown. As the setae grow they twist about in various directions, but never become branched. Septa are formed at short intervals in their older parts.

In describing the perfect sporophore of this plant attention

was called to the threads which radiate evenly from the base of the stipe (*fig. 1*). From the position of these hyphae near the surface of the nutrient medium, and from the fact that they generally terminate in delicate growing points, and are not much interwoven with the threads of the mycelium, it seems that they do not originate from the mycelium, but grow out from the base of the stipe. A study of their origin showed this to be the case. Some of the branches sent out from the hyphae of the young gonidiophore are directed downwards toward the substratum (*fig. 9, b*). These branches were found on many occasions and in all stages of development, from those which had begun to others which had grown to a considerable length. It is interesting to note that those branches destined to grow upward constantly originated just below a septum, while those growing toward the substratum always began above a cross-wall. In many cases observed this was invariably true. Without doubt these radiating branches serve to support the sporophore for, as it often starts from a comparatively small bundle of hyphae, the large head of gonidia with its sterile threads would probably bear it down if it were not strengthened by further support.

The life cycle of this plant seems thus completed. Although many cultures were made in different media no perfect form was obtained, and indeed it seems probable that among some of the more highly developed Hyphomycetes like Trichurus the perfect form has been lost even if it ever existed.

STYSANUS STEMONITES.

Stysanus stemonites is a common form of the Phæostilbeæ[5] found growing on decaying wood and bark of all kinds, on which its small sporophores form gray patches of varying extent. On account of its great resemblance to Trichurus it was grown in a series of cultures parallel with those of the latter fungus, especially as the thought suggested itself that perhaps the sterile bristles might be merely an abnormal production of Stysanus. The cultures for this purpose were obtained from

[5] Sacc. Syl. Fung. 4: 603.

stock tubes in the laboratory. It is needless to say that throughout the cultures the differences between the two forms remained constant. The difference in the size of the two plants alone would be sufficient to remove all doubt as to their specific distinctness. In the course of the cultures, however, so many points of resemblance between the two plants were found, including a small form of fructification new to Stysanus, that it seems worth while to mention them here.

The spores of *Stysanus stemonites* are in general oblong or lemon-shaped, but, as in Trichurus, they are more or less irregular, and extremely variable in shape and size (*fig. 11*). They are usually more pointed than in Trichurus. Under the microscope the spores are dilutely olive-brown, almost hyaline, having the usual dark refractive line around the border. They measure from 6–7μ in length by 3–4μ in diameter, but vary outside of these limits.

Germination of the spores begins immediately after sowing. The process takes place exactly as was described for Trichurus, that is by the formation of a thick primary germ tube (*fig. 12*). After eighteen to nineteen hours the mycelium has reached the stage of development shown in *fig. 14*. The tubes are rather slender, rarely exceeding 3–4μ in diameter. The protoplasm is somewhat indistinctly granular and vacuolate.

The colonies formed by the mycelium are smaller than those of Trichurus of the same age. The hyphae do not show a great tendency to spread out in the agar but remain within a small compass. At the end of four days growth the colonies are scarcely more than 3–4^{mm} in diameter. The mycelium branches abundantly and irregularly, forming a dense mat whose center is raised slightly above the agar. The center is even more stroma-like than in Trichurus. The colonies soon become covered with a gray gonidial growth which extends almost to their margin. This growth consists of Penicillium-like gonidiophores resembling those described for Trichurus. In this case, however they are much more abundant, thus differing in a marked manner from Trichurus, in which they are never sufficiently numerous

to change the external appearance of the colony (*figs. 15, 16, 17*). The gonidiophores themselves, on the other hand, are very much alike in the two plants, as *figs. 15, 16* and *17* will show. In Stysanus also we can find a complete series showing all gradations between these small gonidiophores and the perfect sporophores.

The mature sporophores are small, rarely attaining a height of 0.75^{mm}. They arise either singly from the center of the colony, or several arise together from a stroma-like base. The stipe elongates rapidly, and soon begins to bear basidia and chains of gonidia which remain together in a tangled head so long as they are dry, but when placed in water they break apart instantly. Such sporophores from which most of the gonidia have fallen away are shown in *figs. 20* and *21*.

CONCLUSION.

From this study there can be no doubt of the close relationship of *Trichurus spiralis* and *Stysanus stemonites*. Not only are the perfect forms similar to each other, but they agree closely in their entire development, which may be summed up as follows. The spores germinate in a peculiar manner by means of a stout primary germ tube or proembryo. The mycelium forms a small, compact colony, from which there arises a gonidial fructification very different from the normal fructification of the plants. The normal fruit consists of a bundle of hyphae bearing basidia and chains of gonidia at the summit. All gradations between the simple sporophores and the compound heads exist. The characters which distingish these two plants from each other are the presence of tortuous sterile threads in the head of Trichurus and the difference in the size of the plants and spores. Among these low forms these characters are, perhaps, sufficient for generic separation. The plant treated in the first part of this paper has provisionally been referred to the genus *Trichurus* Clements & Shear. Trichurus was characterized by them thus: "As in Stysanus, but the capitulum densely beset with long strict bristles." The present plant, however, differs from this

description in the possession of curved setae. In order to include this plant in the genus, the generic description would have to be recast as follows: Stroma erect, cylindrical, dark colored, rigid; conidia borne in a loose, oblong head, ovoid or lemon-form, sub-hyaline; head beset with simple or branched, straight or curved, sterile threads or setae. The genus would include the two following species:

TRICHURUS CYLINDRICUS Clements & Shear. Rept. Bot. Surv. Nebraska 4; 7. 1896.

Trichurus spiralis, n. sp.—Sporophores 0.75—3^{mm} high, solitary or in blackish-gray patches: stipe simple or branched, black, composed of many brown septate threads: capitulum shorter than the stipe, cylindrical, obtuse or pointed at the apex, often divided into several smaller heads, beset with simple, brown, septate, tortuous bristles, which are hyaline at the end: gonidia catenulate, oval to oblong, with rounded or pointed ends, often inequilateral or lemon-form, dilutely yellowish-brown, 5–6μ by 2.5—3μ.

On decaying wood, raspberry canes, and on an insect pupa. The plant is easily recognized by the long brown sterile threads in the capitulum.

As was stated at the beginning of this paper, *T. spiralis* was obtained from decaying wood in the autumn of 1898. The same plant had been previously collected here by Professor Atkinson on raspberry canes. Specimens from cultures of this former collection were preserved, and although spores from the older material failed to germinate, the plant was easily identified as being the same as that here described.

BOTANICAL DEPARTMENT, CORNELL UNIVERSITY.

EXPLANATION OF PLATES XXIII AND XXIV.

PLATE XXIII. Trichurus spiralis.

FIG. 1. Perfect sporophore.
FIG. 2. Spores.
FIG. 3. Germinating spores.
FIG. 4. Same forming mycelium.
FIG. 5. Young mycelium.
FIGS. 6–7. Penicillium-fruits.
FIGS. 8–10. Small sporophores; 9*b*, descending branch; 9*a* and 10*a*, ascending branches.

PLATE XXIV. Stysanus stemonites.

FIG. 11. Spores.
FIGS. 12–13. Germinating spores.
FIG. 14. Young mycelium.
FIGS. 15–17. Penicillium-fruits.
FIG. 18. Growing sporophore.
FIG. 19. Same forming gonidia.
FIG. 20. Small perfect sporophore.
FIG. 21. Normal sporophore.

HASSELBRING on TRICHURUS

HASSELBRING on STYSANUS

THE STRUCTURE AND DEVELOPMENT OF THE SPOROPHYLLS AND SPORANGIA OF ISOETES.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.

XVIII.

R. WILSON SMITH.

(WITH PLATES XIII–XX)

(*Concluded from page 258*)

THE SUCCESSION OF SPOROPHYLLS.

THE order of succession of the sporophylls is subject to some variation. It is not at all uncommon, especially in *I. Engelmanni*, to find the regular sequence interrupted by the occurrence of several megasporophylls among the microsporophylls. Occasionally, also, sporangia are found containing both megaspores and microspores. This is rarely the case in wild plants, though quite common, along with other irregularities, in those cultivated in the laboratory. Some plants taken in December, after growing rapidly for seven or eight months in the laboratory, had formed only megasporangia; some others, though producing a few microsporophylls, had failed to bring any microspores to perfection.

The sterile leaves of *I. echinospora* differ from the fertile ones chiefly in their smaller size, the reduction of the sheathing base, and the absence of a developed sporangium. They remain green throughout the winter; while the sporophylls, set free by decay of the base and buoyed up by the gas within the numerous air cavities, are borne away by currents or waves. A close study of the sterile leaves almost always reveals the presence of aborted sporangia. These range in size from a few to many hundred cells; they are often of irregular shape and have lost their protoplasmic contents, though now and then one is found in which a few spores have matured. A longitudinal section of a typical sterile leaf is shown in *fig. 62*, in which the shaded part

represents the undeveloped sporangium. The sterilization of the sporangium does not affect the development of the velum, a fact which supports Hofmeister's view of the primary separation of velum and sporangium. The occurrence of aborted sporangia on so many of the sterile leaves shows that all the leaves are potentially sporophylls, and suggests the probability that Isoetes has retained a more primitive form of the sporophyte than any other vascular plant.

HOMOLOGY OF THE ARCHESPORIUM.

The term "archesporium" was first employed by Goebel (1), who defined it as a cell, cell-row, or cell-plate, from which all the spore-producing cells are formed, and who concluded that in all sporangia the archesporium occupies a hypodermal position. Allusion has been made to the difficulty of accepting this conclusion in such a case as that of Isoetes, but the difficulty is not peculiar to Isoetes. Bower has shown that in several pteridophytes (Selaginella, Equisetum, Lycopodium) the archesporium is not delimited by the first periclinals of the outer layer. How shall we define the archesporium in cases where there is no single hypodermal layer from which the whole mass of sporogenous tissue is derived, and to which the term can be correctly applied as required by etymology and definition? We must either modify our conception of the archesporium or abandon the term altogether as failing to express the facts. It appears to the writer that by changing our notion of the necessary position of an archesporium we could not only avoid this difficulty but would also be enabled to make a more consistent comparison of the sporangia of seed-plants and pteridophytes than is possible with the present nomenclature.

It is pretty generally recognized that there is no true epidermis in pteridophytes. The so-called epidermis is physiologically but not morphologically equivalent to that of seed-plants, for a true epidermis is traceable to a primary layer of the embryo, the dermatogen, which is distinctly present only in seed-plants. As the dermatogen is not represented in pteridophytes, unless it

be in the root-tip, there is consequently no true epidermis, and the part which performs the functions of an epidermis is the outermost layer of the periblem derivatives. Thus, while spermatophytes have three embryonic tissue regions, the plerome, the periblem, and the dermatogen, pteridophytes, with the possible exception of the root-tip, have only the two first-named regions.

The archesporium of all spermatophytes is hypodermal. In no case is it known to be derived from the superficial cells. The epidermis is from the beginning distinct from the inner cells of the sporangium. Though there may be periclinal divisions in the superficial cells, as in gymnosperms, many Ranunculaceæ, etc., these occur only after the differentiation of the archesporium, and the cells so added merely increase the thickness of the wall or apex of the sporangium, but never become part of the sporogenous complex. The true epidermis, set apart at a very early period from the inner tissue of the embryo, is incapable of producing spore-forming cells. That rôle is played by special cells of the outer layer of the periblem.

It is otherwise with the "hypodermal archesporium" of pteridophytes. This is cut off by periclinal divisions from a superficial cell in the case of ferns and Equisetum, and from a group of such cells in the case of the Lycopodiales and Isoetes.

But if the absence of a true epidermis in pteridophytes and the homology of periblem with periblem in all vascular plants are conceded, then the hypodermal cells of spermatophytes are comparable, not to the hypodermal cells of pteridophytes, but to the superficial cells. As we have seen, the sporogenous mass in pteridophytes can always be traced to superficial cells, but in spermatophytes to hypodermal cells and no further; that is, in all cases the function of giving rise to spore-producing cells is localized in certain cells of the outer layer of the periblem.

These facts serve to show the inconsistency of undertaking to limit the archesporium to a hypodermal position in all cases. The cell or group of cells whether superficial or hypodermal, to which in a last analysis all the sporogenous portion of a sporangium can be traced, ought to be called the archesporium. The

change of nomenclature which I would propose, therefore, refers only to the position of the archesporium, and not at all to the meaning of the term. It is simply this: let the term archesporium continue to be used as at present in descriptions of seed-plants, but let it be understood in the case of pteridophytes to signify the superficial cell or cells from which the spore-forming tissue is derived. In this way the difficulties which have been pointed out will all be met, and a better system of homologies can be made for sporangia in general. The archesporium will always occupy the same position relative to the primary meristematic regions, and will be the only part from which the spore-forming tissue arises.

The nomenclature here proposed can be more easily understood by reference to the accompanying diagrams. *Figs. 69* and *70* represent two early stages of the sporangium of a common fern (Pteris), but for the present purpose may be taken as typical of any pteridophyte sporangium. The shaded cell (*a*) would be regarded as the archesporium; it divides into an inner fertile cell (*f*), from which all the spore mother cells are derived, and an outer cell (*s*) which gives rise to a large part of the sporangium wall. In some instances, as we have seen, the separation into fertile and sterile cells is not accomplished by the first division. In such cases there is no contradiction of terms, since all the spores arise from the archesporium. The final condition is the same in all cases, the difference consisting simply in the earlier or later sterilization of the wall region.

Fig. 71 represents a young microsporangium and *fig. 73* a young megasporangium of an angiosperm. The outer layer (*e*), the epidermis, takes no part in the formation of the spore producing cells; *a* is the archesporium, which usually, as in pteridophytes, divides into an outer sterile region (*s*) called the primary tapetum, and an inner fertile region (*f*) called the primary sporogenous cell or cells (*figs. 72, 74*). The name primary tapetum was given to the sterile region to express its supposed function of giving origin to the true or functional tapetum. Enough is now known of the origin of the true tapetum to enable us to say

it has no definite relation to the primary tapetum, and that in fact the term "primary tapetum" is a misnomer. The true tapetum, in many cases at least, is not represented by any morphological structure in the young sporangium.

Is it not possible that the cells *s s* of *figs. 72, 74* represent the wall layer of *fig. 70*, and that the "primary tapetum," in addition to the protective and sometimes nutritive purpose which its derivatives subserve, has also a phylogenetic meaning as a survival of the pteridophyte sporangium wall which has been in great part replaced by the true epidermis? Such at least is the view suggested by a comparison of embryonic organs in general, and of the relations of the primary sporogenous cells.

RELATIONS OF THE VELUM.

On the question whether the velum has any homologue among other plant structures my observations do not furnish any information. It has been compared on the one hand with the indusium of ferns, and on the other hand with the integument of an ovule. The possibility of the latter relation certainly has not been disproved, but the evidence for it is so scant that it must remain merely an interesting suggestion. As to the other relationship, it ought to be borne in mind that the only ferns which can be at all closely related to Isoetes are the eusporangiate families, and all of these bear naked sporangia. The indusium appears in fact to be a special organ of the higher leptosporangiate ferns, without representation in the lower families, such as the Osmundaceæ or in the eusporangiates. This absence of an indusium in the intermediate orders, and the doubtfulness of the homology of the various outgrowths known as indusia, make it impossible to regard the velum and indusium as more than homoplastic structures.

THE AFFINITIES OF ISOETES.

The systematic position of Isoetes has been discussed again and again. By Linnaeus it was placed among the vascular cryptogams, where most later taxonomists have been content to leave it. During the first half of the present century it was most frequently

grouped with the Marsiliaceæ and Salviniaceæ, chiefly on the grounds of their heterospory and hydrophytic habit. DeCandolle was the first to suggest a connection with Lycopodium. In this view he was followed by Brogniart, Endlicher, Hofmeister, and the later German botanists. A summary of the various relationships which have been assigned to Isoetes was given in 1888 by Vines (1), who in the same article put forth the opinion that its affinities are with the eusporangiate ferns, rather than with the Lycopodiales. More recently Farmer (1) and Campbell (4) have expressed their concurrence with this disposition of the genus.

Since this classification has been retained by Vines in his *Text-Book of Botany*, and adopted by Campbell in his *Mosses and Ferns*, it will not be unprofitable to re-examine the evidence, with the purpose of seeing what light can be thrown upon the subject by the present and other recent investigations.

In any discussion of relationships, and especially when there is so great diversity of opinion as in the present case, the conclusion is likely to be a personal one merely, dependent on the kind of evidence which the examiner holds most weighty, rather than on its absolute nature. There are some general principles, however, to which everyone will probably assent, and which ought to govern one in estimating the relative value of the conflicting evidence on which the taxonomist relies. In the first place, the larger the number of characters in which there is agreement, the closer is the relationship, especially if the characters are such as are known to have great taxonomic value in groups related to the one under consideration. Of single characters, those which are most constant are of most value, even though we are not able to detect their special utility. It is generally accepted, too, that those characters which appear in the embryonic stages of an organism serve best to mark its wider relationships, as of class or family, while characters which do not display themselves till later in the individual life are better adapted to distinguish the near relationships of species and genus. This principle applies not merely to the organism

as a whole, but quite as fully to the embryonic stages of its different organs, such as leaf, root, sporangium, and the like.

In conformity with these principles it is proper, in the determination of natural affinities, to place great emphasis upon the reproductive parts, for such parts are found to show very great constancy in their form and occurrence. The sporangia especially, and the form and arrangement of the sporophylls, have long been recognized as of the highest importance. Thus, the classification of the Filicales is largely based on sporangial characters; and the position of the Salviniaceæ and Marsiliaceæ, which was formerly as unsettled as that of Isoetes, was established beyond doubt as soon as the development of the sporangia was fully understood.

It is chiefly on the basis of the superficial resemblances of the sporangia of Isoetes with those of Lycopodium and Selaginella that it has been so long associated with them. If we enumerate the chief differences between the sporangia of Lycopodiales and of ferns, we shall see that in every particular Isoetes agrees with the former. While the Filicales bear numerous sporangia on the dorsal surface of the leaf, Isoetes and the Lycopodiales, with the exception of the Psilotaceæ, the exact relation of whose sporangia to the leaf is still in dispute, bear but one sporangium to a sporophyll, and that on the ventral surface at the base. Such exceptional forms as the Ophioglossaceæ and Marsiliaceæ do not help us in this inquiry. Though it may be true that the whole sporangiophore of the Ophioglossaceæ is, as several morphologists have suggested, the homologue of the single sporangium of Lycopodium or Isoetes, the suggestion is so hypothetical in itself as to give no support to any view based upon it. It is only in the position of the sporangium that these families approach Isoetes; in other sporangial characters, such as number and development, they are like other ferns.

The relative age of the leaves, when the sporangial rudiments first make their appearance, is of considerable significance. In the Filicales, with the exception of the heterosporous forms,

which being leptosporangiate cannot be closely related to Isoetes, the sporangia appear late in the history of the leaf. There is an enormous development of the midrib with its conductive tissues, and of the expanded pinnæ, before the sporangia are recognizable. Nothing is more striking, however, than the quickness with which in the Lycopodiales and Isoetes the rudiment of the sporangium follows the inception of the leaf, which when the sporangium first comes into view is no more than a mere papilla of undifferentiated tissue, without a sign of photosyntactic or conductive tissue.

Still more far-reaching is the agreement of Isoetes with the Lycopodiales in the character of the sporangium rudiment. Goebel (1) in his celebrated paper of 1880–1 classified sporangia as leptosporangiate or eusporangiate according as they arise from single cells or from groups of cells. Though the two classes are connected by transitional forms, such for instance as the Osmundaceæ, in which the sporangia, though always classified as leptosporangiate, do not arise strictly from single cells, the distinction has been approved by all later morphologists. The leptosporangiate plants make a well-defined and consistent group, but the eusporangiates comprise very diverse forms, including the several divisions of seed-plants, the Lycopodiales, the Equisetales, and part of the Filicales. If, however, we leave out accessories, and turn our attention entirely to the essential part of the sporangium, that is to the sporogenous tissue, we find a distinction which has the merit of leaving the Filicales an unbroken group, and of agreeing closely with what is required by a consideration of other characters. This distinction pertains to the origin of the archesporium. The spore-forming part of the sporangium of Isoetes and Lycopodiales can be traced back to a number of cells placed transversely to the leaf, but of all other pteridophytes to a single cell. Is not this distinction as valid as that which pertains to the origin of the whole sporangium? If so, it tends strongly to justify the inclusion of the Lycopodiales and Isoetes within a distinct group set apart from all other vascular cryptogams.

Certain other features of the sporangium of Isoetes find duplication only among members of the Lycopodiales. In all the higher leptosporangiate ferns there is an elaborate mechanism for the bursting of the sporangium and the scattering of the spores. This device, consisting of a row of peculiarly thickened cells (the annulus), and a group of cells which form an easy place of rupture (the stomium), is very rudimentary in the lower leptosporangiates (Osmundaceæ), and in the Ophioglossaceæ and Marattiaceæ, but it is not altogether absent. There is at least a predetermined line along which dehiscence shall take place. The elaboration of this dehiscence apparatus is one of the chief peculiarities of the higher leptosporangiates. When we turn to the Lycopodiales and Isoetes, however, we find positively no contrivance for dehiscence, and no vestige of an annulus or stomium. The sporangium wall is simple, and bursts by desiccation in Lycopodium and Selaginella, and by decay in Isoetes; and neither method can be regarded as a specialization.

Another analogy has been brought to light by Bower's discovery in Lepidostrobus of certain radiating strands or processes in the sporangium which are regarded by him as very probably of the nature of trabeculæ. Since the relationship of Lepidostrobus to Lycopodium can hardly be doubted, there is here a point of contact with this group of plants in a feature in which otherwise Isoetes stands alone.

Again, Selaginella and Isoetes agree very nearly in the manner of selection of the megaspore mother cells. The unselected mother cells do not divide at all, and all the spores resulting from the division of the fertile ones as a rule reach maturity. In heterosporous ferns all the mother cells divide into spores, of which but one becomes a megaspore. The contrast may be expressed in the statement that the megasporangium is differentiated in Isoetes and Selaginella *before* the tetrad division, but in heterosporous ferns not until *after* that division.

The persistence of the tapetum in Lycopodiales and Isoetes is a character to which no great importance is to be attached, for

tapetal characters are notoriously variable. Such bearing as it has, however, is in harmony with what may be inferred from other features of the sporangium. It involves no disorganization of the cells, no multiplication of nuclei except as related to cell-division, and no mingling of naked protoplasm with the young spores.

One of the facts which Vines advanced as an argument against the usually accepted classification of Isoetes is the absence of a strobilus, the characteristic arrangement of the sporophylls in the Lycopodiales. He contrasts also the elongated, slender, branched stem of Lycopodium or Selaginella with the short unbranched stem of Isoetes, which much more closely resembles that of some eusporangiate ferns. It may be doubted whether such superficial characters, unless accompanied by internal features of which they are the outward expression, have any value in settling the relationship of distinct genera or families. At all events, their usefulness in angiosperm taxonomy is limited to the distinction of species; they would be of no use in deciding the family to which an undetermined species ought to belong. I am inclined to think the whole plant-body of Isoetes can best be explained as a shortened strobilus, just such as Lycopodium would become by suppression of the stem and axis, while allowing a normal development of the leaves and sporangia.

The most obvious diagnostic character of the three groups of pteridophytes is furnished by the leaves. The leaves of the Isoetes are *sui generis*, and afford little ground for associating it with any one group rather than another. Though they are relatively few and large, as is the case among ferns, their unbranched outlines and simple tissues show an analogy with the leaves of Lycopodiales; while their peculiar vascular bundles, and chambers, and diaphragms remove them as effectually from either group. There is record, it is true, of a fossil Isoetes with a branched leaf, indicating, when taken in conjunction with the sudden reduction of the vascular bundle just above the ligule, the possibility that the present form of the leaf may be a reduced one representing a more complex ancestral type. But

we must admit, so far as mature leaf structures are concerned, that Isoetes occupies an isolated, and in no sense an intermediate position.

The testimony of the young leaves, however, is not so neutral. The form of the leaf rudiments, their manner of growth, and arrangement about the axes are the same in Isoetes as in Lycopodium and Selaginella, and quite different from what is seen among ferns. The difference is not fully expressed in saying that in one case the leaf originates from a single apical cell, and grows by means of it, and that in the other case the initiative is from a group of cells. The leaves of ferns are distinctly acrogenous, which method of growth gives them the power of assuming complex forms and allows the successive and often slow formation of stipe, pinnæ, and pinnules, and their gradual unfolding. A leaf which grows as does that of Isoetes has its power to assume a complex form limited to the time when it is meristematic throughout; as soon as the apex becomes permanent tissue the outline of the leaf is determined. The difference between such leaves is fundamental and far-reaching. A Lycopodium leaf could easily attain the size of an Isoetes leaf by retaining the meristematic power for a longer time, for they differ only in degree. The leaf of a fern could become like that of Isoetes, or *vice versa*, only by a radical change in the manner of growth.

The similarity of the leaf rudiments of Lycopodium and Isoetes is only a particular instance of a general likeness which extends to all their embryonic organs. We have already seen how this is true of the sporangia; and it holds equally good for the roots[1] and stem apex. In none of these organs is there ever an apical cell or any concentric segmentation of the apices, such as are characteristic of all the Filicales and Equisetum. A difference in this respect in the case of apical-growing organs, like the roots and stem, may not lead to important differences in the mature structures, as the variation in the stem apices of Selaginella suffices to show. But a comparative examination of

[1] Van Tieghem (1), but Bruchmann (1) entertains a different view.

meristems was shown by Bower to possess considerable phylogenetic value, in the case of ferns, and to lead to results which agree with those arrived at by a comparison of other characters. The fact that Bower has since changed his view with regard to which type of fern is more primitive does not in any way lessen the value of his previous conclusions. If we extend the series made out by him it would be in this order: typical leptosporangiate ferns, Osmundaceæ, eusporangiate ferns, Selaginella, Isoetes, and Lycopodium. In this connection the dichotomy of the roots of Isoetes, Lycopodium, and Selaginella ought not to be overlooked.

The ligules of Selaginella and Isoetes were by Goebel made the ground for grouping the two genera into one order, the Ligulatæ, though the classification was recognized by its proposer as merely one of convenience. In the former part of this paper I have made a comparison of these organs, and expressed the view that their similarity is sufficient to demonstrate their homology. If this view is correct, it furnishes additional support to the relationship of Isoetes and the Lycopodiales, especially in consideration of the discovery of a ligule in the vegetative leaves and the sporophylls[2] of Lepidostrobus, another lycopodiaceous plant.

Turning now to the gametophytes, we notice that when Vines suggested the connection of Isoetes and ferns, it was supposed that important differences existed between the female gametophytes of Isoetes and Selaginella; but the later and more complete investigations of Heinsen (1) and Arnoldi (1) have demonstrated their close resemblance. The diaphragm of the female gametophyte of Selaginella is not a true septum, and does not arise as Pfeffer (1) supposed it did, by the division of the spore into two cells. In both Isoetes and Selaginella, the free division of nuclei, their parietal placing, and the gradual extension of cell division from the periphery to the center of the spore are the same, and have no counterpart in the germination of the megaspores of heterosporous ferns. The gametophytes agree also in the absence of chlorophyll.

[2] Maslen (1).

Nearly similar evidence is furnished by the male gametophyte. Though Belajeff (1), to whom we owe the most exact investigation of the subject, says the male gametophytes of Isoetes and Selaginella afford little ground for relating the two genera, he has shown several points of resemblance, such as the separation of the prothallial (or rhizoidal) cell from the single antheridium by a cellulose wall, and the final dissolution of the non-cellulose septa of the antheridium wall, so that the spermatozoids float free in the cavity of the spore.

Though not disposed to place much dependence as a clue to the working out of phylogenetic relationships among heterosporous plants on such structures as archegonia and antheridia, which must necessarily conform more or less in shape to the space in which they are confined, I find some interest in the fact that Isoetes and Lycopodium are the only genera of pteridophytes in which the occurrence of more than two neck canal nuclei has been reported, and that in Isoetes, as in *Lycopodium Phlegmaria* and Equisetum, the plane of the division of the primary neck canal nucleus is at right angles to the archegonium axis.

The two characters which stand most in opposition to the inclusion of Isoetes in the group Lycopodiales are its multiciliate spermatozoid and the embryogeny of its sporophyte. Campbell has very properly emphasized the similarity of the Isoetes spermatozoids to those of ferns. It requires only a brief survey of the plant kingdom to show the great constancy of the form and behavior of male cells in different classes of plants. Consider, for example, the non-motile spermatozoids of the Florideæ, or the biciliate spermatozoids of bryophytes. Accordingly, if we still classify Isoetes among Lycopodiales, we must admit that the multiciliate spermatozoids make an exception to a constancy which is otherwise remarkable. Unfortunately, we have only Lycopodium and Selaginella for comparison, and are still in ignorance as to what the gametophytes of the other genera may have to tell us.

The embryo of Isoetes finds its nearest approximation in Botrychium[3] though the resemblance may be only an external

[3] Jeffrey (1).

one, due to the late differentiation of the embryonic organs and the suppression of the stem, rather than to any deep-seated likeness. However that may be, the suspensor of Lycopodium and Selaginella is a positive morphological character separating them from Isoetes. Probably the embryos of Isoetes and Botrychium can be looked upon as generalized types, the specialization taking the form in ferns of a very early demarcation of the embryonic organs, and in Lycopodium and Selaginella of a suspensor.

Two other possible reasons for relating Isoetes to ferns deserve a passing mention. Of the connection between the velum and the indusium enough has already been said; and of the agreement of the stems of Isoetes and Botrychium it is sufficent to say that the agreement is simply in the fact of secondary thickening.

The claim that Isoetes is the genus of modern pteridophytes which makes the closest approach to angiosperms, particularly to monocotyledons, gives it an interest quite out of proportion to its numerical representation. It is not clear, however, that the claim is well supported by facts. Unquestionably Isoetes and Selaginella, in their heterospory, and their intrasporic and reduced gametophytes, exhibit features of life history which run closely parallel to that of seed-plants; but such features really foreshadow monocotyledons no more than they do other seed-plants. The hypodermal archesporium, and the origin of the megaspore mother cell as the lowest of a row resulting from periclinal divisions of an archesporial cell—two points which my observations disprove — would, if established, be as strong proof of a gymnosperm as of an angiosperm attachment. Some facts distinctly favor the gymnosperm connection; these are the manner of germination of the megaspore, and the method of selection of the megaspore out of a large mass of potentially spore-producing cells, as in Cycas, Callitris, etc., to which may be added whatever favors the relationship of Isoetes with the Lycopodiales.

Professor Campbell has shown that the embryo of Isoetes bears a likeness to that of a monocotyledon in having a lateral

stem apex and a terminal cotyledon, and suggests a comparison with the embryo of Alisma for instance. The resemblance in form is undoubtedly very close, but we ought not to overlook some equally important differences. The entire absence of a suspensor in Isoetes, which has been brought forward as an objection to its close affinity with Lycopodium, militates quite as strongly against an affinity with monocotyledons; and the foot, which is particularly well developed in Isoetes, cannot be said to have any clear representative in monocotyledon embryos.

In general habit Isoetes has been compared to some grasses, rushes, and the like; this is a mere external resemblance in one of the most adaptive features of plants, and not supported by internal and essential similarities. A similar objection can be raised to the comparison of the stelar regions of Isoetes and of such monocotyledons as Dracæna. In the latter it is true there is a secondary thickening carried on by means of an extra stelar "cambium," but this cambium merely adds parenchymatous tissue within which separate vascular bundles are organized; there is nothing strictly comparable to the prismatic zone or central xylem cylinder of Isoetes. Even were the likeness much closer than it is, the peculiar stem of Dracæna, Yucca, etc., is so certainly a newly acquired, and not a primitive character, that it affords no sound reason for deriving monocotyledons through an Isoetes-like type.

To one who has followed this discussion thus far it will be evident that in the writer's opinion the balance of evidence is in favor of relating Isoetes to Lycopodium and Selaginella rather than to eusporangiate ferns. Of course the facts are not all in hand as yet, and new discoveries may materially affect the aspect of the case. The facts which the present investigations have brought to light certainly tend in the one direction. The mode of origin, development, position, and general characters of the sporangia, the development of the leaf, and the nature of the ligule point to the correctness of including Isoetes among the Lycopodiales; while the form of the spermatozoids and

embryo show the necessity of making it a separate family. The Lycopodiales so constituted comprise six genera pretty widely separated in morphological characters, as from the antiquity of the group one might naturally expect. But the extreme differences are not greater than in the Filicales. If we can include Azolla, Marsilia, the common ferns, Hymenophyllum, the Marattiaceæ, and the Ophioglossaceæ in one group, it ought not to appear inconsistent to include Psilotum, Lycopodium, Phylloglossum, Selaginella, and Isoetes in a group of coordinate rank. A fuller knowledge of the three little-known genera may tend to confirm this view, especially if they depart as widely from the remaining genera in other characters as in general habit and sporangia; but if their gametophytes, spermatozoids, and embryos agree very nearly with Lycopodium and Selaginella, it will probably be better to make of Isoetes a fourth group of pteridophytes equivalent in rank to the three now universally recognized. If an affinity with seed plants must be sought, the evidence points to a connection with gymnosperms rather than with monocotyledons.

SUMMARY.

1. The stem apex lies at the bottom of a funnel-shaped depression, around the sides of which the leaves are arranged spirally. This depression is produced by the expansion of the cortical cells of the stem in all directions.

2. The leaves arise as crescent-shaped bands of meristematic tissue. At first the basal part of the leaf (the sheath) grows most rapidly; afterwards the region of growth is transferred to the part above the ligule. There is no persistent or sharply-marked zone of meristem. The whole leaf is meristematic at first; it then gradually passes into permanent tissue, the change beginning at the apex and extending gradually downwards.

3. The air-cavities are formed out of four longitudinal bands of cells, which after losing their contents and power of multiplication are ruptured into transverse partitions by the growth of the other parts of the leaf. The size, but not the number of the air-cavities, increases with the age and growth of the leaf.

4. The ligule originates in a single vesicular cell as described by Hofmeister. The mature ligule can be distinguished into four regions: (1) the sheath which has its origin in the lowermost cells of the young ligule, (2) the glossopodium, (3) a region of living cells, and (4) a region of disintegrating cells.

5. The rudiment of the sporangium is a transverse row of superficial cells below the ligule; the upper part of this gives rise to the velum, the lower part to the sporangium proper.

6. There is no definite hypodermal archesporium. The middle cells of the sporangium *Anlage* are the first to undergo periclinal divisions. Additions to the sporogenous complex are made from the superficial cells of the sporangium.

7. The general direction of growth of the sporangium is at right angles to the face of the leaf, with a slight tendency in young sporangia to an upward direction. The cells are not in well-arranged rows or stratified layers.

8. There is no evidence that certain of the archesporial cells give rise to trabeculæ only, and certain others to mother cells only. The trabeculæ and megaspore mother cells or groups of microspore mother cells greatly outnumber the archesporial cells.

9. There is no evidence that each of the primary cells of the sporangium pursues an independent growth. On the contrary, their derivatives blend indistinguishably.

10. The microsprangia and megasporangia are indistinguishable until they have attained a volume of 15,000–25,000 cells.

11. The sporangium becomes recognizable as a microsporangium by its differentiation into irregular deeply-staining and feebly-staining radial bands. The deeply-staining regions after a period of active multiplication become the mother cells. The feebly-staining regions become the trabeculæ, walls, and tapetum,

12. The tapetum is organized out of the layer of sterile cells adjacent to the mother cells; its cells are small, densely cytoplasmic, and persistent.

13. The middle cells of the trabeculæ become elongated by compression and growth; their nuclei also become elongated and spindle-shaped.

14. The outer wall of the microsporangium is usually four layers thick, the innermost layer being part of the tapetum. The inner wall, that is the cells between the base of the sporangium and the vascular bundle, is probably formed by sterilization of cells derived from the primary cells of the sporangium.

15. The divisions of the microspore mother cells may be either successive or simultaneous. The two spindles of the second division do not become connected by secondary fibers. The microspores are usually bilateral but sometimes tetrahedral.

16. The number of microspores in a sporangium is 150,000–300,000.

17. A sporangium first becomes recognizable as a megasporangium by the marked enlargement of many or most of the cells of about the third and fourth layers. All such enlarged cells are to be regarded as potential mother cells, and the number of them which succeed in producing megaspores is probably dependent on nutrition. No tabular tapetal cells are cut off in connection with the development of the megaspore mother cells, nor is the megaspore mother cell the innermost of a row of cells formed from a single archesporial cell in a manner comparable to what is seen in the ovules of seed-plants.

18. Many cells which enlarge almost to the size of mature mother cells are finally unable to give rise to spores, but divide up into smaller cells which ultimately form part of the tapetum.

19. The trabeculæ, tapetum, and walls arise in the megasporangium as in the microsporangium, the chief difference being the greater massiveness of the single trabeculæ in the former and the much greater abundance of the tapetum.

20. No details of the division of the megaspore mother cell were obtainable. The megaspores are usually tetrahedral in arrangement, but occasionally bilateral. The number in a sporangium is 150–300.

21. The first leaves of a season are megasporophylls, and these are succeded by microsporophylls. There is occasionally some irregularity in the order of succession, and sometimes a sporangium is found which bears both kinds of spores.

22. The sterile leaves in a majority of cases have aborted sporangia. When these have made any considerable development they are usually found to show the characters of megasporangia.

23. The sporangia after all cell divisions have ceased continue to increase in volume, apparently by the osmotic properties of the substances surrounding the young spores.

24. An attempt to relate the change from megasporophylls to microsporophylls to an exhaustion of the nutritive cortical cells formed in the preceding year was unsuccessful.

25. To secure a more consistent nomenclature it is proposed to employ the term archesporium in speaking of a pteridophyte sporangium to designate the superficial cell or cells from which the sporogenous tissue takes its origin.

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EXPLANATION OF PLATES XIII–XX.

The drawings, except *fig. 1*, have been made with the aid of a camera lucida, and all have been reduced by photography to two fifths of their original size. Both in the text and in the explanation of the plates, the terms transverse, longitudinal, and tangential, when used to describe sections of the ligule and the sporangium are to be understood as indicating the planes in which the sporophylls were sectioned.

FIG. 1. Base of microsporophyll, inner face showing the sporangium (*s*), the velum (*v*), and the ligule (*l*). × 4.

FIG. 2. Radial longitudinal section of base of sporophyll; *s*, *v*, *l*, as in *fig.* 1. × 5.

FIG. 3. Longitudinal section of apex of a small plant. × 48.

FIG. 4. Longitudinal section of apex of a larger plant; *x*, the tracheids, *p*, the prismatic layer, *t*, the leaf traces, *m*, the cambium (semidiagrammatic). × 48.

FIG. 5. Part of the prismatic ring as seen in transverse section of the stem; *x*, *p*, *t*, *m*, as in *fig. 4*. × 160.

FIG. 6. Cortical cells from the neighborhood of the cambium. × 240.

FIG. 7. Cortical cells from the outer region of stem. × 240.

FIG. 8. Longitudinal section of a number of young sporophylls; the sporangia are indicated by the dotted outlines. × 48.

FIG. 9. Cross section of a young leaf above the ligule. × 300.

FIG. 10. Cross section of a young leaf more advanced than that shown in *fig. 9*; the position of the future air chambers is shown by the groups of nearly empty cells; the small circles of *figs. 9* and *10* indicate the side towards the axis of the plant. × 300.

FIG. 11. Part of a longitudinal section of a leaf more advanced than that of *fig. 10*, showing origin of the air cavities; *p*, the phloem, *x*, the xylem. × 300.

FIGS. 12–13. Transverse section of leaf with the vesicular cell from which the ligule originates. × 300.

FIG. 14. First division of the ligule, sectioned in plane *a*—*a* of *fig. 15*. × 490.

FIG. 15. First division of the ligule seen in radial longitudinal section. × 490.

FIGS. 16, 18. First division of terminal cell of ligule sectioned in plane *a—a* of *fig. 15*. × 490.

FIG. 17. The same sectioned in plane *b—b* of *fig. 15*. × 490.

FIG. 19. Tangential section of older ligule. × 490.

FIG. 20. Transverse section of ligule of same age as that of *fig. 19*. × 490.

FIG. 21. Transverse section of still older ligule. × 300.

FIG. 22. Median radial longitudinal section of base of half-grown ligule; *s*, the sheath, *g*, the glossopodium, *v*, the velum. × 490.

FIG. 23. Radial longitudinal section of base of mature ligule at the position indicated by *a—b* of *fig. 25*, showing the thickened cells of the velum and leaf adjacent to the ligule. × 48.

FIG. 24. The same in *I. Engelmanni*. × 48.

FIG. 25. Transverse section of ligule and leaf at the position indicated by *a—b* of *fig. 23*. × 30.

FIG. 26. Median radial longitudinal section of young sporophyll, showing rudiment of the sporangium. × 490.

FIGS. 27–28. The same more advanced. × 490.

FIG. 29. Transverse section of young sporophyll with sporangium. × 490.

FIG. 30. Transverse section of sporangium more advanced. × 490.

FIG. 31. Tangential section of young sporangium. × 490.

FIGS. 32–38. Radial longitudinal sections of young sporophyll; *fig. 37* is a section through the side of the sporangium of which *fig. 36* is a median section; *v*, the velum, *g*, the glossopodium, *s*, the sheath. × 490.

FIG. 39. Transverse section of sporangium more advanced. × 490.

FIG. 40. Transverse section of leaf with sporangium of same age as that of *fig. 39*. × 490.

FIG. 41. Median radial longitudinal section of a sporangium of about the same age as the last. × 490.

FIG. 42. Longitudinal section of side of sporangium. × 490.

FIG. 43. Transverse section of a sporangium still older but in which the trabeculæ are not yet recognizable. × 490.

FIG. 44. Transverse section of young leaves and of microsporangium at the time of the first differentiation of fertile and sterile regions; the shaded portion represents the fertile region; *v*, the velum, *l*, the ligule, *f*, the vascular bundle. × 48.

FIG. 45. Oblique nearly tangential section of microsporangium. × 48.

FIG. 46. Tangential section of microsporangium. × 30.

FIG. 47. Cross section of sporophyll and microsporangium, showing the trabeculæ, tapetum, *t*, and a few microspores; *v*, the velum (semidiagrammatic). × 30.

FIG. 48. Portion of microsporangium at the time of the first differentiation of fertile and sterile regions. × 490.

FIG. 49. The same, showing portion of outer wall. × 490.

FIG. 50. Portion of an older microsporangium, showing differentiation of sterile regions into trabeculæ and tapetum (*t*). × 490.

FIG. 51. Portion of trabecula, tapetum (*t*), and young spores of a microsporangium. × 490.

FIG. 52. Part of outer wall and tapetum (*t*) of nearly mature microsporangium. × 490.

FIGS. 53–55. Division of mother cells to form microspores; *fig. 53* illustrates successive division; *fig. 54*, simultaneous division; *fig. 55*, the shape of the spores, bilateral in *a* and *b*, tetrahedral in *c*. × 490.

FIG. 56. Young microspores. × 490.

FIG. 57. Cross section of megasporangium with young spores and tapetum (*t*). × 48.

FIG. 58. Portion of a trabecula and tapetum (*t*) of a megasporangium, × 490.

FIG. 59. Tetrahedral arrangement of young megaspores. × 490.

FIGS. 60–61. Successive division of megaspore mother cells, spores bilateral. × 490.

FIG. 62. Median radial longitudinal section of sterile leaf with aborted sporangium (shaded).

FIG. 63. Transverse section of megasporangium first distinguishable as such. × 490.

FIG. 64. Part of transverse section of a megasporangium with a group of potential mother cells. × 490.

FIG. 65. The same with a single mother cell. × 490.

FIG. 66. Part of a transverse section of a megasporangium; for explanation see text. × 490.

FIG. 67. Diagram of young megasporangium.

FIG. 68. Diagram of a longitudinal section of the stem. See p. 228.

FIGS. 69, 70. Early stages of the sporangium of a fern. Diagrammatic. *a*, archesporium; *f*, fertile sporogenous cell; *s*, sterile wall cell.

FIGS. 71, 72. Early stages of a microsporangium of an angiosperm. Diagrammatic. *a*, archesporium; *e*, epidermis; *s*, primary tapetum; *f*, primary sporogenous cell or cells.

FIGS. 73, 74. Early stages of a megasporangium of an angiosperm. Diagrammatic. Letters as in *figs. 71, 72*.

BRIEFER ARTICLES.

PHYSIOLOGICAL NOTES. I.

1. Soja beans for imbibition experiments.

NO SEEDS, unless they have been killed, are suitable for the demonstration of imbibition except when the experiment is to run for a short time, as for a single day. But for such brief experiments — and they are as good as longer ones — the Soja beans are an especially interesting subject, because of their pronounced change of shape in swelling. The three diameters may be designated as D, the longest one, passing between the cotyledons, at a right angle with D', which also passes between the cotyledons, but through the hilum, and D'', which passes through the cotyledons. The average lengths of these in ten air-dry beans were: D, 0.30734 inch; D', 0.28061 inch; D'', 0.22583 inch. After soaking twenty-four hours in distilled water at 14° C., the measurements were: D, 0.53708 inch; D', 0.34193 inch; D'', 0.2651 inch. The increase had been: D, 74.75 per cent., D', 21.85 per cent., D'', 17.39 per cent. I have never seen a change in shape comparable to this in the swelling of any other hard and solid substances. The swelling at first is more uniform in all directions, so far that D'' is occasionally greater when imbibition is a little over half complete than when it is finished (!), though the seed coats are not wrinkled when this occurs. The increase in bulk of these beans was very nearly 150 per cent., while the increase in weight was only 133 per cent. (the dry beans are very heavy).

Working on the micellar hypothesis, we expect the power to conduct heat in any direction to vary somewhat inversely to the power to absorb water: since the greatest swelling will be in the direction of the least axes of the micellae, where the proportion of surface to mass is greatest, while heat is conducted most easily lengthwise of the micellae, in the direction of fewest breaks. Thus heat travels most readily lengthwise in wood, at a right angle to the line of greatest swelling. I tested it with these beans by the usual method, melting a very thin layer of paraffin on the surface, and sticking a hot needle in the

middle. On the smooth surfaces, where the cotyledons meet, the melted area is even in outline and easy to see. Average dimensions of ten such melted areas were: along axis D, 0.0649 inch; along D', 0.0714 inch. The diameters of the cells which conduct the heat are about equal in these two directions. The cells are elongated along the axis D'', but the cotyledons cannot be cut so as to give a surface smooth enough to work with. The result — conduction more difficult in the direction of greater swelling — harmonizes with the hypothesis. But it is hard to imagine an arrangement of the micellae by which their long axes are, for instance, parallel in the entire cellular structure, without regard to the individual cells.

2. Gas diffusion through the cuticle.

Experiments on the diffusion of carbon dioxide through the cuticle are interesting in relation to the gas nutrition of the plant, and have an even greater value as aids in the explanation of the most fundamental physical processes. For we are almost obliged to preface our treatment of osmosis with a rehearsal of the mechanical theory of gases: and then we are too apt to introduce into the particular explanation of osmosis a new element, in the semi-permeable membrane. The plant cuticle is an appropriate instance of a membrane nearly semi-permeable to gases. With the leaves usually employed the experiment is very slow, and I have tested a number of leaves in search of some one with which the course of the experiment would be enough more rapid to recommend it for class demonstration.

All the leaves in the following lot have the stomata confined to the lower surface, and are available for winter use. They were set up in the usual way: a cork fitted over one end of a glass tube, and heated in paraffin, and the leaf sealed over the hole in the middle of the cork. On each leaf all except an area of $121^{sq\ mm}$ over the hole was covered with paraffin. Of course it was necessary to have the upper surface of the leaf exposed, instead of placing it next the cork, as Detmer recommends for single experiments. The tubes, all 21^{cm} in length, were then filled with mercury, which was displaced in a mercury bath with carbonic acid. As only a comparison was sought, barometric readings were neglected: the temperature was reasonably constant. All were in the same mercury bath. The experiment began January 8. The height of the mercury column under the various leaves was as follows:

	Jan. 9, 1 P.M.	Jan. 10, 1 P.M.	Jan. 11. 3 P.M.	Jan. 12, 4 P.M.	Jan. 13, 3 P.M.	Jan. 15, 3 P.M.	Jan. 17, 4 P.M.	Jan. 20, 3 P.M.
Ficus (immature)	21 mm	26 mm	35 mm	42 mm	46 mm	58 mm	66 mm	73 mm
Begonia: smooth, green	18	—	30	36	36	37	43	44
Begonia: red	31	ruptured						
Hedera	27	leaked						
Cyclamen	38	61	90	110	120	140	158	184
Farfugum	34	56	70	98	118	145	157	170
"Croton" (Codiaeum)	65	123	153	168	177	184	185	184

The see-sawing, especially evident with the Cyclamen and Farfugum leaves, is a mystery. From other experiments I know that diffusion through the Hedera leaf is considerably faster than through mature leaves of Ficus. Nerium leaves are also among the more resistant. The resistance to diffusion increases with the age of the leaf and with its dryness. According to Detmer dry Hedera leaves are impermeable; but air-dry and entirely brown leaves of Ficus still permit a slow escape of CO_2. From these and a few other experiments I regard the Croton[1] leaf as the best adapted of the leaves of ordinary greenhouse plants for the demonstration within a reasonable time of the diffusion of gases through the cuticle.

What the actual process of the passage of any gas through the cuticle is would be hard to determine. Of course it is not mere diffusion, else the oxygen and nitrogen of the atmosphere would pass more rapidly than the heavier carbonic acid. It may be that they dissolve in the cuticle, the carbon dioxide much more readily: or possibly they enter into some loose chemical combination, as oxygen is taken up and given off by haemoglobin. However that is, the fact that it was under the same leaf that the mercury rose fastest, and began to fall first is probably due to its thin cuticle, so that any gas must traverse it but a short distance. And in any case the external factors governing the rate of passage would be the same.

If it is desired merely to show how fast carbon dioxide can pass through a plant membrane, without concern as to the immediate application of the experiment to ordinary plant problems, one of the water lilies is a still better subject. It should be fixed with the under surface exposed to the air. With all other conditions the same as in the other experiments, and with part of a leaf of *Nymphæa alba* as the closing membrane, the mercury rose 185 mm in four hours! In three days it passed 190 mm.

[1] The plants commonly known in greenhouses as Croton are really Codiæum.

Most physical chemists agree that so long as the semi-permeable membrane really allows none of the solute to permeate it any resistance it may offer to the passage of the solvent is without influence upon the osmotic pressure. Ostwald,[2] Speyers,[3] and Pfeffer[4] make the same statement. The argument — and it a perfect one — is, in brief, that the osmotic pressure is the aggregate impact of the molecules of the solute against a medium which they cannot permeate: this medium must contain, and hence be permeable to, the solvent, else the solute could not touch it: but as the solvent has no share in the actual pressure, it is indifferent whether its movement be free, or barely possible. Osmotic pressure, in this sense, is computed from boiling and freezing point determinations: it cannot be directly measured. *The osmotic pressure useful in plant cells*, and the osmotic pressure measured by so-called osmometers, *is not the pressure which the flying molecules of the solute exert against the restraining membrane* (or other medium), *but it is the pressure which this membrane passes along against some other, more resistant medium*, or the solvent in question which is outside it. And this practical, available osmotic pressure depends very largely upon the resistance offered by the membrane to the passage of the solvent. If several osmometers be set up with the same solution, osmosis to take place through equal areas of different membranes, it will be found after a time that the columns of liquid they support are far from equivalent. In each osmometer the height of the column measures the pressure then available for work; but it may be objected that the experiment is not yet complete.

In a plant all the osmotic pressure which does anything — whether it is to keep the plant fresh and stiff (turgescent), or to absorb water from the soil, or to transport water or food, or to fulfill an usual condition of growth — is the pressure of the protoplasm against the cell wall. If there is an increase in the osmotically active material in the cell sap, *i. e.*, in the pressure of the sap against the vacuole wall, the promptness with which there can be a corresponding increase in the

[2] OSTWALD: Solutions 103.

[3] SPEYERS: Text-book of physical chemistry 63.

[4] PFEFFER: Pflanzenphysiologie 1:120 [2 ed.]. Zur Kenntniss der Plasmahaut und der Vacuolen, etc., 302. 1890. "Die Qualität der Haut kann, so lange gelöste Stoffe nicht exosmiren, den osmotischen Druck nicht beeinflussen und meine frühere gegentheilige Annahme, die sich der allgemein verbreiteten Vorstellung anschloss ist demgemäss irrig."

pressure against the cell wall depends on how rapidly water can get into the sap, and this in turn depends, inter alia, upon the resistance the protoplasm offers to its passage; this is very slight, but still must be something. Now in practice the osmotically active matter in the sap varies constantly,[5] and therefore the osmotic pressure available for work does depend constantly upon the ease with which water traverses the semi-permeable membrane.

To return to the osmometer: the column of liquid supported rises more slowly in some cases than in others because the membrane offers greater resistance to the movement of water through it. It seems evident to me that, if the osmotic pressure is the only force at work, there will be a certain minimum of pressure below which it would not suffice to put the water in the membrane into motion at all. And in this case the height at which the column finally comes to rest will measure the total impact of the molecules against the membrane *minus* the resistance the membrane offers to the passage of the solvent. Whether the movement of the water in the membrane by its own "living force" will be more inward than outward until the entire theoretical osmotic pressure gets expression in the column supported, I do not know, but doubt it: and anyway that would be by the introduction of another source of energy. Talk is not likely to get far on a subject where there have been no experiments for twenty-three years, but it is about all that we have, pro or contra. So long though as he based his opinions on experiments, Pfeffer thought that the pressure was influenced by the resistance of the membrane. And Krabbe[6] says that at temperatures near the freezing point a state of equilibrium is reached while there is a decided tension between the periphery and axis of a cylinder of live pith submerged in water, because of the resistance to the passage of water through the outer cells.

All these considerations apply equally to the tubes closed by a membrane permeable only to the gases on one side. And the fact that the "Croton" leaf did not keep its lead does not destroy my position, because the inward diffusion of the gases of the atmosphere is a

[5] As by movement of salts or food, formation or hydrolysis of starch, etc. As I found some years ago, the turgor in the leaf of Funaria is regularly higher at night, by the pressure of 0.5 per cent. KNO_3, than it is in the morning.

[6] KRABBE, G.: Jahrb. f. wiss. Bot., **29**: 447. 1896. As the water drawn in by osmosis is held by imbibition in the wall, the experiments on imbibition are valid for osmosis. Review in BOT. GAZ. **23**: 303. 1897.

disturbing element which prevents our seeing just what would happen if the carbon dioxide were the only diffusing gas in the question; it is a case where the membrane permits some of the solute to escape.

The fact that carbon dioxide diffuses more rapidly through a cuticle if the latter is kept moist, shows that water also can pass through it, and, therefore, that in the case of a solute which cannot permeate it, the cuticle would serve as the semi-permeable membrane of an osmometer. I have set one up, using a leaf of Farfugum as the membrane, and 20 per cent. NaCl as the solution inside. It was a week before any endosmosis was apparent, and in three weeks the column rose barely 6^{mm}. I believe that though this cuticle be absolutely impermeable for the salt, such a resistance as it opposes to the water must prevent its use for the accurate measurement of osmosis.—EDWIN BINGHAM COPELAND, *University of West Virginia, Morgantown*.

A NEW SPECIES OF PUCCINIA.

Puccinia Thompsonii, n. sp.—III. Epiphyllous or occasionally amphigenous. Sori scattered, oblong to linear-oblong, 0.25–6^{mm} long, reddish to chestnut-brown, erumpent, the ruptured epidermis flanking the sides. Spores oblong-clavate, constricted at the septum; vertex rounded or sometimes obtusely pointed, thickened; base obtusely rounded; epispore rather thin, very smooth, color golden-brown or lighter, 48–68 × 15–24. Pedicel slender, hyaline, 1.5–2.5 times the length of the spore.

On *Carex stenolepis* Torr. (*C. Frankii* Kunth). Lebanon, Ind., Mar. 19, 1891, *J. C. Arthur;* Pine Lawn (St. Louis), Mo., spring of 1894, *C. H. Thompson;* Alexandria, Ind., Sept. 23, 1898, *Miss Lillian Snyder;* Greencastle, Ind., Oct. 1898, *L. M. Underwood;* Pine Lawn (St. Louis), Mo., Jan. 2, 1899, *Hume & Thompson.*

This species somewhat resembles *P. Bolleyana* Sacc., but differs from it in the more scattered, larger, oblong, lighter-colored sori and the somewhat longer and narrower spores. The epispore of the upper cell is not quite so much thickened. The species is named for C. H. Thompson, of the Missouri Botanical Garden, who first called my attention to it. In the above description the material from St. Louis is taken as the type, as its abundance has furnished ample material for study. However, the material collected at the several points in Indiana, above cited, shows no appreciable variation. I am indebted

to Dr. J. C. Arthur for kindly comparing this with other possibly allied species and for material contributed.—H. HAROLD HUME, *Lake City, Fla.*

THE TAXONOMIC VALUE OF THE STAMINATE FLOWERS OF SOME OF THE OAKS.

(WITH EIGHT FIGURES)

THE flowers of the oaks have received comparatively little attention from investigators in systematic botany. Most authors have described the flowers of a single species, usually *Quercus alba*, which they have considered as a type for the entire genus. Sargent in his *Silva* has given a brief description of the flowers of each species, but the degree of variation in the form of the lobes and the amount of pubescence is hardly touched upon.

The present study was undertaken in order to determine whether there was not a wider range of forms among the flowers, and, if so, whether this variation is constant enough to aid in the separation and limitation of the species. For this purpose the staminate flowers of the oaks in the Cayuga Flora (*Q. acuminata*, *Q. alba*, *Q. platanoides*, *Q. Prinus*, *Q. macrocarpa*, *Q. rubra*, *Q. coccinea*, and *Q. velutina*) were chosen.

Staminate flowers were collected from as many trees of each species as possible at anthesis. The flowers were opened, the stamens removed, and the perianth mounted in glycerine jelly. In order to determine the limits of the midrib it was found of assistance to warm the slide after mounting.

The oaks may be divided into two groups, one containing those which require a single season for maturing their fruit, the other requiring two seasons. Of the oaks enumerated above the first five belong to the first group, the last three to the second. This same division is substantiated by a study of the floral organs.

The first group has a six-lobed perianth that is campanulate to rotate, and has six to nine stamens. The second group is easily distinguished from the first by its closely companulate perianth, and the stamens are four or five in number. The different species in each group may be distinguished by the size and shape of the lobes, the amount of pubescence, and the presence or absence of a midrib.

QUERCUS ACUMINATA.—This species has a six-lobed, thin, and delicate rotate perianth, which is 3^{mm} in diameter. The lobes are usually

somewhat unsymmetrical, two or three being close together and separated by narrow sinuses, the others are more widely separated and the sinuses are correspondingly wider and deeper. This appearance is often due to tearing in mounting, but the natural lobing may be determined by tracing the cilia along the margin. The lobes are ovate to lanceolate and obtuse. One of the lobes is frequently somewhat broader than the others, and once or twice notched near the apex. The midrib is distinct and extends a little over one third of the length of each lobe. The perianth is pilose, and the hairs are usually tinted with red. The bract is persistent, and adheres closely to the flower when the latter is removed from the catkin. This is the only species of this region that does not lose the bract before the maturing of the flower.

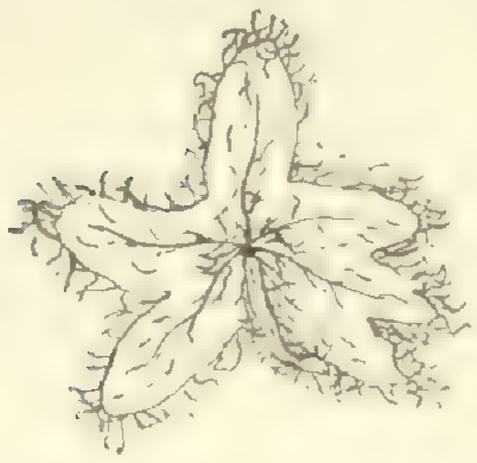

FIG. 1.—*Q. acuminata.*

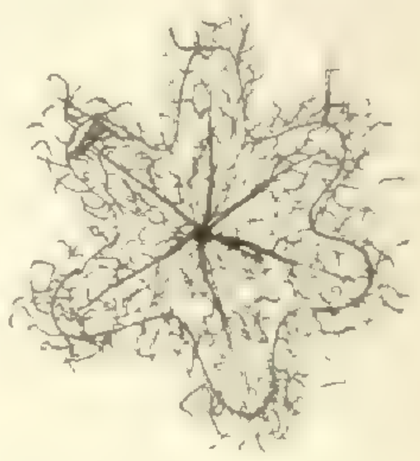

FIG. 2.—*Q. alba.*

QUERCUS ALBA.—The flowers of *Q. alba* are very symmetrical in outline, thus forming a strong contrast to the preceding species. The perianth is slightly campanulate, thin, delicate, and five or six-lobed. The diameter is 2–3^{mm}. The lobes are small, broadly oval to ovate, and obtuse. The midrib is prominent and distinct nearly to the apex of the lobes. The perianth is densely pilose, the hairs being long and matted, rendering it difficult to spread the flower without tearing.

QUERCUS PLATANOIDES.—The flowers of *Q. platanoides* are only about one half the size of those of *Q. alba*, being 1–2^{mm}, but resemble them closely in other respects. The texture of the perianth is thicker. It is rotate rather than campanulate, and forms a flat six-lobed disk at the base of the stamens. The lobes are broadly oval to ovate, and separated by broad and obtuse sinuses. The midrib is distinct nearly to the apex of each lobe. The perianth is pilose, but the hairs are not so thickly matted as in *Quercus alba*.

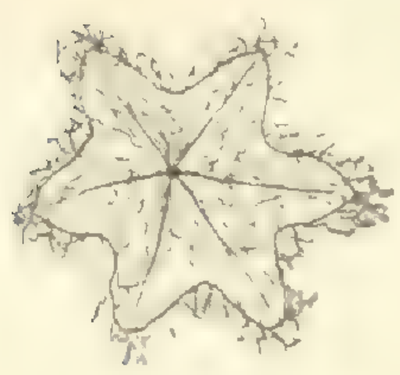

FIG. 3.—*Q. platanoides.*

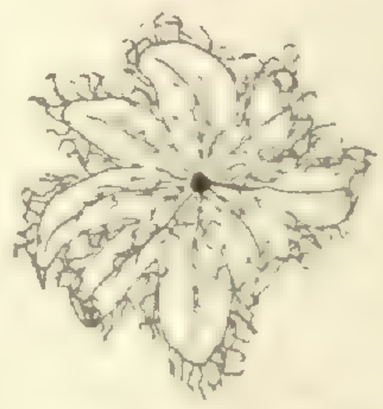

FIG. 4.—*Q. Prinus.*

QUERCUS PRINUS.—The perianth of *Q. Prinus* is small, thin, and deeply lobed. The diameter is from 2–2.5^{mm}. It resembles the flowers of *Q. alba*, but the sinuses are much deeper and narrower, and the

lobes are more spatulate or obovate. There is also a variation in the number of lobes; in the majority of flowers examined there were from six to eight, but occasionally one was found with as many as ten. The midrib is distinct at the base, but disappears near the apex of the lobes. The perianth is sparingly pilose, with the lobes ciliated by long slender hairs, giving it a very shaggy appearance.

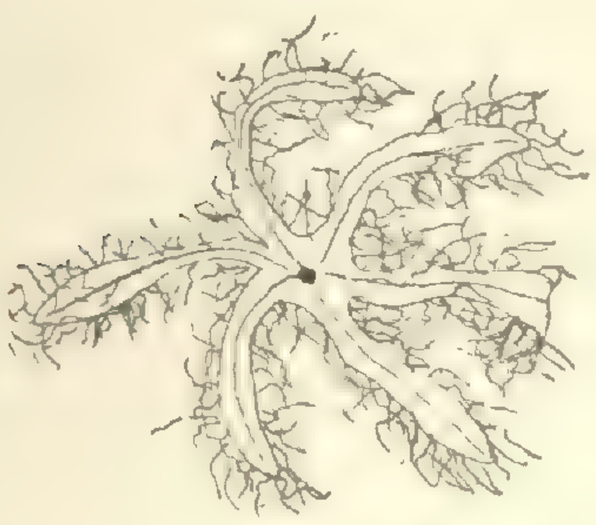

FIG. 5.—*Q. macrocarpa.*

QUERCUS MACROCARPA.—*Q. macrocarpa* has a very characteristic flower. It is more deeply lobed than any of the preceding species, the sinuses extending nearly to the point of attachment. It is the largest of this group, having a diameter of 3–3.5^{mm}. The lobes are long and very narrowly linear, five or six times as long as they are wide, and are frequently slightly curled or twisted, making it difficult to separate them from the filaments of the stamens. The midrib is distinct to the apex of the lobes. The perianth is pilose, the hairs being very long and shaggy.

FIG. 6.—*Q. rubra.*

QUERCUS RUBRA. The flowers of *Q. rubra* are much larger than any of the other forms studied, having a diameter of 4–4.5^{mm}. They are campanulate and indistinctly five or six-lobed. As the flowers develop the stamens push through the narrow throat and tear the perianth into uneven segments varying in number from two to six. The midrib is distinct and slightly thickened at the base, but becomes indistinct about half way to the apex of the lobes. The perianth is nearly smooth or slightly pilose, and the lobes are thinly ciliate with long hairs.

FIG. 7.—*Q. coccinea.*

QUERCUS COCCINEA.—*Q. coccinea* has a perianth that very closely resembles the one just described, although the other characters of the tree are more frequently confused with *Q. velutina* than with *Q. rubra*. The perianth is campanulate and slightly six-lobed, with a diameter of 3.5–4^{mm}. Its four or five stamens as they develop tear it into two or three irregular segments. The midrib is distinct at the base but very soon disappears. The perianth is pilose, and there is a thicker row of cilia along the margin than was found in *Q. rubra*.

QUERCUS VELUTINA.—The last of this series, *Q. velutina*, has a very closely campanulate, thin and delicate perianth. The diameter is the same as in *Q. coccinea*, 3.5–4^{mm}. The midrib is entirely wanting. The perianth is pilose, and the cilia along the margin are long and matted. The throat of the perianth is so narrow that it is torn by the stamens, as soon as they begin to develop, into two or three nearly equal segments. In the majority of cases the perianth had separated into two equal segments, but occasionally one was found with three, never with more.

FIG. 8.—*Q. velutina.*

The results of this study show that there is marked variation among the flowers, not only in the case of the large groups, but also among the species in each, and the following key was based on these characters:

KEY TO NATIVE OAKS BASED ON THE STAMINATE FLOWERS.

A. *Stamens six to nine.*
  I. Bract persistent after anthesis . . . . *Q. acuminata*
  II. Bract deciduous before anthesis.
    a. Perianth deeply lobed.
      1. Lobes narrowly linear . . . . . *Q. macrocarpa*
      2. Lobes obovate or spatulate . . . . . *Q. prinus*
    b. Perianth with shallow lobes.
      1. Perianth slightly campanulate: diameter 2–3^{mm} . *Q. alba*
      2. Perianth rotate: diameter 1–2^{mm} . . . *Q. platanoides*

B. *Stamens four or five.*
  I. Midrib wanting . . . . . *Q. velutina*
  II. Midrib present.
    a. Perianth pilose . . . . . *Q. coccinea*
    b. Perianth smooth with lobes thinly ciliate . . *Q. rubra*

—W. W. ROWLEE and SUSIE P. NICHOLS, *Cornell University.*

OPEN LETTERS.

PROFESSOR W. PFEFFER AND THE ACTIVE ALBUMIN.

THE recent publication of the second edition of Pfeffer's *Physiology of Plants* in English[1] contains on pages 67–69 the same erroneous statements and ideas in regard to the active albumin studied by Bokorny and myself as does the original German edition published two years ago: which induces me to make the following remarks.

Those who are particularly interested in the matter are referred to the protest I published two years ago under the title "Ueber Protoplasma und actives Eiweiss, zur Abwehr."[2] I have since published an extensive description of the chemically labile protein stored up as reserve material in many vegetable objects, a protein which easily changes chemically into an insoluble compound, and coagulates under the same conditions that cause the death of the protoplasm, although more slowly. This detailed account, the result of work through a long series of years, is contained in chapters nine and ten of my treatise "Die chemische Energie der lebenden Zellen."[3]

Pfeffer has wrongly interpreted or apparently overlooked certain chemical phenomena. Pfeffer's conscience seemed, however, to have dictated as a sort of excuse the following passage in the preface of his above mentioned work: "Still I am afraid that in spite of all my care much has been forgotten or overlooked, especially since, owing to the pressure of other duties, the time necessary for this work has been obtained with difficulty. This has rendered it *impossible for me to study certain problems as deeply as I had wished.*"—OSCAR LOEW, *Agricultural Department, Washington, D. C.*

[1] PFEFFER, W.: The Physiology of Plants, translated by Alfred T. Ewart. Oxford. 1900.

[2] Botanisches Centralblatt 74 : 5. 1898.

[3] München, 1899, E. Wolff, publisher. In a more condensed form it was published in London, 1896, under the title "The Energy of Living Protoplasm." Kegan Paul, Trench, Trübner & Co.

CURRENT LITERATURE.

BOOK REVIEWS.

Elementary text-books.

PROFESSOR Atkinson's *Lessons in Botany*[1] is announced as an abbreviated and simplified edition of the author's *Elementary Botany*, reviewed in this journal for December 1898. The design is to meet the requirements of those secondary schools, still far too numerous, in which not more than a half year is given to botany. The contents are clearly separated into three uses: "exercises for the pupils, demonstrations by the teacher, and descriptive matter for reading and reference." The book is more than a mere condensation of the larger one, for a large part of the matter has been rewritten, new illustrations have been introduced, and the whole presentation has a different constituency in view. As was said in the former review, Professor Atkinson is a very successful teacher and has had much experience with the schools, so that this book, as well as the other, should prove of large service in introducing into the secondary schools the truer views of botany which they so much need.—J. M. C.

AN author who writes from a university standpoint for the secondary schools has a difficult task. His own breadth of knowledge, and his relation to his fellow-workers invite to a broad, comprehensive, and up-to-date treatment of his subject. The secondary school, on the other hand, insists upon a work that is elementary in fact as well as in name.

The *Outlines of Plant Life*[2] is another expression of the desire on the part of teachers of botany to present the subject to the secondary schools in such a manner as to indicate in some measure the present condition of the science, and at the same time to give a usable book. Its appearance as an abridgement of *Plant Life* is a recognition of the fact that the present need of the secondary schools is a simpler and less comprehensive treatment of the subject. Almost a third of the original text, with the accompanying illustrations, has been cut out; some of the introductory portions have been rewritten, summaries added to each chapter, and appendix I (Directions for laboratory study) has been incorporated with the text as exercises. These changes certainly render the book much better adapted to the work of the secondary

[1] ATKINSON, GEORGE FRANCIS.—Lessons in botany. Small 8vo. pp. xv + 365, *figs. 277*. New York: Henry Holt & Co. 1900.

[2] BARNES, CHARLES REID. Outlines of plant life. Small 8vo. pp. vi + 308, *figs. 250*. New York: Henry Holt & Co. 1900.

school. The rearrangement of the laboratory work is particularly commendable. The logical arrangement, clear treatment, and freshness of the larger book are retained in this volume. There is still left a heavy year's work for a good teacher and a strong class, and it is the judgment of the reviewer that further simplification might have been secured by the less minute treatment of some subjects, as the root, movement of plants, growth, and ecology, admirable as those subjects are in their present form. The many good points of the book will commend it to secondary teachers, whose class room experience alone can determine its fitness to survive.—I. N. MITCHELL, *State Normal School, Milwaukee, Wis.*

The white pine.[3]

THE white pine has always commanded more than its share of study because of its economic importance. In so far as Professor Spalding and Dr. Fernow have succeeded in explaining the geographic and edaphic factors which control its distribution, they have made a valuable contribution to ecology and plant geography. The large number of acre-yield tables of measurements and explanations of soil and forest conditions enable them to draw certain definite and scientific conclusions regarding the causes of distribution.

The leading ecological factor is the nature of the soil and the water content of the same. While adapting itself to almost any variety of soil, the white pine prefers one with a fair admixture of sand, insuring a moderately rapid drainage. This is a soil intermediate between the stiff clayey soil on one hand, where the deciduous forest predominates, and the dry, light sandy, coarse and gravelly soil on the other hand, where the red pine (*Pinus resinosa*) and the jack pine (*Pinus Banksiana*) seem able to outdo it. The shallow root system of the white pine permits it to occupy the thinner soils of the rocky slopes in the Adirondacks and New England states.

Light is another important ecological factor. Compared with other pines the white pine has great shade endurance, hence its admixture with maples and beech, where it has an equal chance in open places. But white pine seedlings are never found in the dense shade of the hardwood forest; in such a place there is little hope for the white pine to gain a foothold. Owing to this inability of the white pine seedling to maintain itself in the dense shade, the hardwood forest is gradually encroaching upon it, except in soils too poor for the development of the deciduous forest.

A carefully prepared map of the geographic distribution offers a foundation for the discussion of the climatic factors governing such distribution.

[3] SPALDING, V. M.: The white pine. Revised and enlarged by B. E. FERNOW. Contributions on insect enemies of the white pine by F. H. CHITTENDEN, and on the wood of the white pine by FILIBERT ROTH. Bulletin no. 22. U. S. Department of Agriculture, Division of Forestry. 4to. pp. 185. *pl.* —. 1899.

It is pointed out that the white pine is delimited by conditions of humid and cold atmospheres such as are found in northern latitudes and high altitudes. Its distribution is perhaps more dependent on humidity than on temperature, or rather on a low transpiration factor, that is, such a relation of heat and moisture, both at the foot and at the top, that the thin foliage can readily perform its function.

Besides the distribution of the white pine, the monograph treats of the white pine lumber industry, the original stand and present supplies, the morphological characters, the seed and seed supply, the structure and development of the wood, the growth and development in open stand and in the forest, growth in volume, the yield of white pine, and dangers and diseases. Contributions by two specialists on insect enemies and wood of the white pine add to the economic interest. The appendix, which comprises more than half the monograph, consists of seven sets of tables of measurements, and a careful explanation of the forms used in the investigations.—H. N. WHITFORD.

MINOR NOTICES.

AMONG THOSE who have taken advantage of the offer of the Division of Forestry to make a personal study of areas which offer favorable opportunities to illustrate forest management are the owners of two large tracts of land in the Adirondacks. The results of the investigation are embodied in a recent bulletin[4] of the Department. The author makes a plea for an American system of forestry. He discusses six measures of prime importance for the proper care of the European forest, though they would be exceedingly impracticable if applied to the plots under consideration, and then proceeds to propose a simple system of management that will enable the owner to make a profit from the land and at the same time secure the permanence of the forest.

Among the features of great interest to the ecologist is the special consideration of the spruce. Under this head the habits of the spruce, the influence of situation and soil on its character and distribution, its tolerance of shade, and its reproduction are discussed in a clear and scientific manner. Another valuable feature is the presence of a large number of illustrations, mainly from photographs, and of two contour maps of the regions described. —H. N. WHITFORD.

DR. C. F. MILLSPAUGH has issued as Vol. II, no. 1, of the Botanical Series of the Field Columbian Museum the first part of his *Plantae Utowanae*, being a catalogue of the species. The plants were collected between December 1898 and March 1899 in Bermuda, Puerto Rico, St. Thomas, Culebras, Santo Domingo, Jamaica, Cuba, The Caymans, Cozumel, Yucatan, and the

[4] GRAVES, HENRY S.: Practical forestry in the Adirondacks. Bulletin no. 26, U. S. Department of Agriculture, Division of Forestry.

Alacran shoals, during the Antillean cruise of the yacht Utowana. An itinerary gives information as to the time devoted to each station, and a second part will contain a detailed account of the ecological observations, and also the plates made from the many fine photographs secured. The list of species is surprisingly long when one considers the shortness of the time and the often unfavorable conditions for collecting. Thirty-four new species are described, distributed from the fungi to the Compositae.—J. M. C.

MR. E. W. HERVEY, of New Bedford, Mass., has published independently his observations on "The colors of flowers."[5] In it he records a large amount of work which might have been better directed had he made himself familiar with the rather extensive literature on the subject. In a section on the sequence of color he assails with a vigor and directness worthy of a better object the shallow generalizations of Grant Allen on this subject. His presentation has no logical sequence and no definite marshaling of the many discrete facts which he has gathered respecting the relation of insects to color, nor any adequate correlation of these facts with the host of previous observations.—C. R. B.

THE MOST recent fascicles of Engler and Prantl's *Natürlichen Pflanzenfamilien* are nos. 193 and 194. The former contains the conclusion of Plectobasidiineæ (Sclerodermineæ) by ED. FISCHER, and the beginning of *Fungi imperfecti* by G. LINDAU. The Sphæropsidales are taken up, the 107 genera of Sphærioidaceæ being presented, and the Nectrioidaceæ begun. No. 194 contains the conclusion of Polypodiaceæ, Parkeriaceæ, Matoniaceæ, Gleicheniaceæ, Schizæaceæ, and Osmundaceæ, all by L. DIELS, and the beginning of Hydropteridineæ by R. SADEBECK.—J. M. C.

NOTES FOR STUDENTS.

SOME INTERESTING NOTES on *Arceuthobium pusillum* have been published by Hermann von Schrenk in *Rhodora* for January.

PROFESSOR J. M. HOLZINGER has found *Grimmia teretinervis* Limpr. growing near Winona, Minn. The species is new to North America.

AN ANNOTATED LIST of the puff-balls, slime-moulds, and cup-fungi of Orleans county, New York, has been published by Dr. Charles E. Fairman, of Lyndonville, in Proc. Rochester Acad. Sci. 3: 206–220. 1900.

DR. ROLAND THAXTER continues to discover new Laboulbeniaceæ. In a recent paper he describes 68 new species and 7 new genera of this family. This great extension of our knowledge of these fungi is in part the result of an examination of insect collections in the British and Paris Museums from all over the world, and of material from correspondents, as well as that gathered by the author in Maine, Florida, and elsewhere.—C. R. B.

[5] 8vo. paper, pp. 105, *figs.* 3.

MM. RENAULD and CARDOT describe in the ninth fascicle of their *Musci exotici novi vel minus cogniti*[6] a large number of species of mosses of Costa Rica and Mexico.—C. R. B.

DR. A. W. EVANS has published[7] a monograph on the Hawaiian Hepaticae of Schiffner's tribe Jubuloideæ, with full descriptions and sixteen admirable plates. Eight new species are described. The collections of Mr. C. M. Cooke, Jr., made in the summers of 1897, 1898, and 1899 mainly on Oahu and Kauai have furnished a large amount of interesting material.—C. R. B.

THE farmer's bulletin no. 112,[8] on *Bread and the principles of bread making*, prepared by Helen M. Atwater, is botanical in so far as it deals with yeasts and the structure of grains. Both these topics are treated most inaccurately. Indeed the whole bulletin strikes one as an inexpert compilation which experienced bread makers will laugh at and the inexperienced consult in vain for help.—C. R. B.

MR. R. G. LEAVITT has published[9] the results of some experiments to determine whether or not the roots of orchids and the shoots of Tillandsia, Sphagnum, and Leucobryum could condense water vapor from moist air. His results confirm those of Nabokich, published shortly before,[10] and it now seems highly improbable that the structures like the velamen of orchid roots and the hyaline cells of sphagnum are adapted to secure water in the form of vapor.—C. R. B.

A PECULIAR embryo-sac in *Peperomia pellucida* is reported by D. H. Campbell.[11] The megaspore originates in the usual way, but after the third division of the megaspore nucleus the eight nuclei are arranged about the periphery of the sac without any suggestion of polarity or differentiation in egg-apparatus, antipodals, and polar nuclei. The most striking fact is that still another division takes place, giving rise to sixteen nuclei, which are also arranged about the periphery of the sac. One of the nuclei in the micropylar end of the sac enlarges somewhat, and is to be regarded as the egg nucleus, but there are no distinct synergids, and no antipodals, although there is some grouping of a variable number of nuclei in the chalazal end of the sac. In one case the male nucleus, which is small and somewhat spirally coiled, was observed within the egg. The first division of the embryo, which has no

[6] Bull. Soc. Roy. Bot. Belg. **38**: 1–48. (Paged 1–48, and bound in second fascicle of vol. 38, but not continuous with remainder of fascicle.)

[7] Trans. Conn. Acad. Sci. **10**: 387–462. *pls. 44–59*. 1900.

[8] U. S. Dept. of Agriculture.

[9] Rhodora **2**: 29, 63. 1900.

[10] Résumé in BOT. GAZ. **29**: 222. March 1900.

[11] Ber. d. deutsch. bot. Gesell. **17**: 452–456. *pls. 31*. 1899. See also Ann. Bot. **13**: 626. 1899.

suspensor, is vertical, and the second transverse. In the ripe seed the embryo fills the entire sac, but no organs are differentiated. The free nuclei of the embryo-sac never divide, but the perisperm performs the function of endosperm. The writer regards Peperomia as a transition form between angiosperms and lower seed plants or perhaps higher pteridophytes. It is a very old type, and apparently should be placed at the beginning of the angiosperms.—CHARLES J. CHAMBERLAIN.

RECENT STUDIES on the conidia of the Entomophthorales by Cavara[12] have shown two types in the structure and development of these organs. The conidia of *Empusa muscæ* are multinucleate, for the conidiophores are characteristically cœnocytes, and the constriction of the conidium from the tip always includes a mass of dense protoplasm with a number of nuclei. The nuclei are said to fragment in the conidia, dividing by constriction in the middle. On germination the conidium puts forth a tube, and the multinucleate protoplasm streams forward into it. The conidia of *Entomophthora Delpiniana* are uninucleate, perhaps for the reason that the conidiophores show a distinct tendency to pass from the condition of a cœnocyte to that of a segmented branched filament. The greater portion of the contents of the terminal cells, with a single nucleus, passes into a bud-like process which becomes cut off below by constriction to develop the conidium.—B. M. DAVIS.

IN a recent number of *Science*,[13] Professor C. S. Slichter of the University of Wisconsin proposes to use the kinetoscope for the reproduction and magnification of slow motions such as the growth, development, and movements of plants, flow of plastic substances, etc. His suggestion seems so likely to prove fruitful that we reproduce part of his note.

> The method that I selected . . . . was as follows: Let the moving body be photographed upon kinetoscope film at stated intervals — every few minutes, or every few hours, as the case may require. After a sufficient number of these photographs have been obtained, the film may be run through an ordinary projecting kinetoscope at the usual rate. In this way the motion that has required several weeks for its production may be reproduced upon the screen within the limits of a few minutes or seconds. I have magnified in this way the rate of motion about 500,000 fold, but of course there is no major limit to the possible rate of magnification. I made the first application of this method of magnifying slow motions to the motion of growing seedlings. Several peas and beans were placed in a glass root cage containing wet sand. The photographs were taken by artificial light at fixed intervals day and night for about three weeks. When the film is run through the kinetoscope the entire growth for the period of three weeks is reproduced in a few seconds. . . . . The kinetoscope also shows very clearly the different speeds at which the various parts of the plant grow.

[12] CAVARA: Osservazioni citologiche sulle Entomophthoreæ. Nuovo Giorn. Bot. Ital. 6: 411. 1899.

[13] Science 11: 535. 6 Ap. 1900.

and the different speeds at which the same part grows at different times. The greatest variety in the rate of growth exists, as I suppose is well known, and of course the kinetoscope brings out the relative rates of growth in a very truthful and graphic manner. . . . . At the present time I am preparing some additional films taken from growing seeds. Of course there is no reason why the photographing should not be continued until the plants have bloomed and fruited, if any fact important to mechanics or botany is likely to result from the trouble. Perhaps botanists know of matters in plant growth and plant development that it may pay them to investigate by the same method. I anticipate that some interesting facts concerning the mechanics of the root's motion into and through the soil will result from such studies.

MR. ALBERT F. WOODS, of the U. S. Division of Vegetable Physiology and Pathology, has found that chlorophyll is rapidly destroyed by oxidizing enzymes, which are normally present in small quantity in many of the higher plants. Under unknown conditions these enzymes become more active or are produced in larger quantity, causing disease marked by variegation, such as the mosaic disease of tobacco, which may be produced at will by inoculation with germ-free virus from diseased areas, and by cutting back healthy pot-grown plants which have about exhausted the soil in the pot and allowing only one shoot to develop rapidly in a high temperature under copious watering. The lighter areas invariably show the presence of larger amounts of some substance which turns a solution of gum guaiac blue. This reaction Mr. Woods accepts as indicating the presence of oxidizing enzymes, though aware that it has been considered unreliable. The oxidase and peroxidase may remain in soil uninjured for several months. The latter diffuses readily in plant tissues or agar plates, and may be dried without injury.[14]

In a short note in *Science* 11: 17–19. 1900, Mr. Woods presents reasons for believing that in the mosaic disease of tobacco leaves the lighter colored areas contain more starch than the healthy tissues because the greater amounts of oxidase they contain partly or wholly inhibits the action of translocation diastase.—C. R. B.

PROFESSOR D. H. CAMPBELL has published some of the results of his studies of Araceæ in the current *Annals of Botany* (14: 1–25. *pls. 3*. 1900). Species of Dieffenbachia and Aglaonema were the forms from which he obtained the most complete results, although very many gaps remain to be filled even in them. In both of these cases the axial origin of the ovule seems undoubted, and this probably represents a primitive condition. One of the most striking facts presented by these forms, as well as others of the family, is the early development of a compact endosperm which completely fills the sac, and in some cases is probably developed before fertilization, and certainly often appears when no embryo is formed. In the whole family there is also a tendency for the antipodal cells to develop strongly, often dividing

[14] Centralbl. f. Bakt. 5^2: 745–754. 1899.

and forming a tissue which supplements the endosperm. The embryo is also somewhat peculiar and suggestive. The failure to develop a suspensor is thought by Professor Campbell to be associated with the complete investment of the embryo by the endosperm. Two types of segmentation of the young embryo which were noted are: (1) the formation of two transverse divisions before any longitudinal walls appear, and (2) a regular quadrant formation suggestive of the first divisions of the fern embryo. The cotyledon is exceedingly large as compared with the stem and root, the last organ appearing late and being rather lateral in origin, as in Lysichiton and Pistia.

One of the peculiarities of Dieffenbachia is that the single archesporial cell divides transversely very unequally, the outer cell being the larger and becoming the embryo sac. The inner cell may divide once or not at all. The embryo sac in its development encroaches upon the whole of the nucellar tissue and finally is in contact with the inner integument. A nucellar cap, however, remains at the micropylar end of the sac, and its cells enlarge and divide, forming a somewhat permanent tissue, and suggesting the condition of things which Smith has found in Pontederiaceæ and Merrell in Silphium.

The characteristics of the group which have been developed so far, and which the author regards as primitive, are the axial ovule, the early development of a solid endosperm, the great development of the antipodal cells, and the absence of a suspensor.—J. M. C.

A NEW GENUS of the Volvocaceæ from the streams of central Illinois, has been described by Kofoid[15] and named *Platydorina*. It forms a flat horseshoe-shaped colony of sixteen or thirty-two cells, the plate being somewhat twisted into a left spiral. The rounded side of the outline is the anterior end, and the portion corresponding to the heel of the horseshoe is prolonged into three or five tails, hence the name of the single species, *P. caudata*. The contents of the cells are bright green, and each has a pair of cilia and generally the red pigment spot. The tails are formed of intercellular gelatinous matter, and they, with the peculiar twist of the colony, present the most prominent specific characters. No method of sexual reproduction has been discovered.

The asexual reproduction is by the repeated division of gonidial cells in the whole or part of the parent colony. The early stages of this segmentation are identical with those of Eudorina and Pleodorina. The colony becomes cup-shaped, then ellipsoidal, but finally flattens so that the cells from two sides are pressed together. They become intercalated in a common plate, in such a regular manner that every alternate cell has the cilia and pigment spot uppermost to the observer, while the other cells present the

[15] KOFOID: On Platydorina, a new genus of the family Volvocidæ, from the plankton of the Illinois river. Bull. Ill. State Lab. of Nat. Hist. 5, 1899.

view with the pyrenoid most prominent. From this method of development it would appear that Platydorina is not a more specialized Gonium, but derived from ancestors of the Eudorina type. Platydorina is positively phototactic, exhibiting this habit to a conspicuous degree, but avoiding bright sunlight. The movement is always forward unless obstructions are met, and the rotation as a rule is from right over to left. This is the direction naturally favored by the resistance that the water offers to a moving body twisted in the manner of this coenobium. However, as the rotation in Pleodorina and Eudorina is predominately from right over to left, it is possible that the form of the colony in Platydorina is the result and not the cause of this rotation. Dr. Kofoid discusses the use of the term colony, as unfortunately inappropriate to the higher members of the Volvocaceæ, where there is a certain degree of cell differentiation, especially in Pleodorina and Carter's form of Eudorina, with the probability of a physiological cooperation between the cells of Volvox. Which facts make this group of plants a most interesting one from a speculative and evolutionary standpoint, and perhaps we may pardon their failure to accommodate themselves to a system that makes possible the use of exact terms.—B. M. DAVIS.

NEWS.

PROFESSOR O. MATTIROLO, of Florence, has been appointed professor of botany in the University of Turin.

DR. HUGO ZUKAL, associate professor of botany in the Agricultural Institute at Vienna, died on February 15, at the age of 55.

PROFESSOR A. N. BERLESE, of Bologna, has been appointed assistant professor of botany and director of the botanical institute, at Sassari, in Sardinia.

DR. EDWIN B. ULINE has been appointed special assistant in the Gray Herbarium for the summer, during the absence of Dr. B. L. Robinson in Europe.

PROFESSOR M. A. BARBER, associate professor of botany in the University of Kansas, will spend six months in Berlin in bacteriological study. He will resume his university duties in the autumn.

THE MARINE BIOLOGICAL LABORATORY offers this summer for the first time a course in nature study. It is to occupy the entire session of six weeks, and will be conducted cooperatively by members of the staff of the laboratory and a number of specialists. The thoroughness characteristic of the work of this institution is thus assured. We note among those outside of the staff the names of Wheeler, Dudley, and Peckham in entomology; Chapman, Herrick, Stone, and Dearborn on birds; Hodge on the toad; Patten on the king crab; Scott and Penhallow in paleontology; and McFarlane in phanerogamic botany. It is quite safe to say that never before in this country has a course in nature study been presented by a group of men so strong in their respective lines. The time will be divided as follows: cryptogamic botany one week, phanerogamic botany one week, the king crab two days, insects four days, birds one week, the toad one day, marine invertebrates one week, animal psychology six days. A few sentences from the introduction to the program, written by Dr. Whitman, shows the temper of the course: "We shall have field work, laboratory exercises, lectures, demonstrations, and all available means of reading a few chapters in nature's book. Study nature for understanding, not for information, is the ideal to be kept in view. Those who are ambitious to fill their notebooks with a complete survey of the field of facts are advised not to apply. We shall be content if we succeed in taking a few soundings at advantageous points." Announcement of the course may be obtained from Dr. Bradley M. Davis, University of Chicago.

AFTER OCCUPYING for twelve years small and in many respects unsuitable rooms in the old college buildings, the botanical department of University College, Liverpool, is at length to be housed in a new and commodious institute, the munificent gift of Mr. W. P. Hartley, of Aintree, Liverpool. The building is 37 by 85 feet, and five stories high. The museum will con-

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tain not only morphological specimens illustrative of the scientific aspect of botany, but also specimens of all products of the vegetable kingdom used in the arts, such as timbers, pharmaceutical products, cottons, hemp, flax, food-products, both in the raw and in the manufactured state. There is also provided an ample equipment of lecture halls, herbarium rooms, elementary laboratories, and also laboratories for research in morphology and physiology. Mr. Hartley's gift will provide University College, Liverpool, with a botanical laboratory worthy to stand alongside the pathological and physiological laboratories, the recent gift of Mr. Thompson Yates to the college. The building will in all probability be ready for occupation before the beginning of the autumn of 1901.

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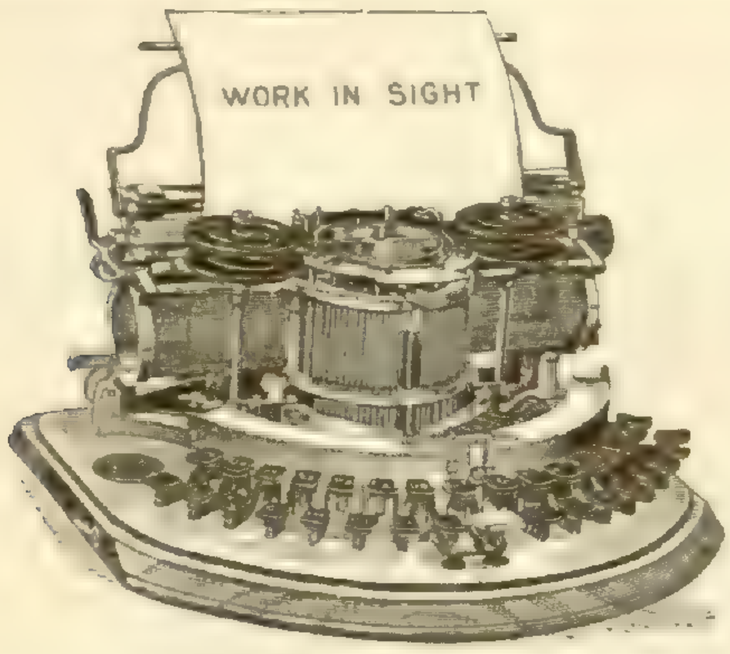

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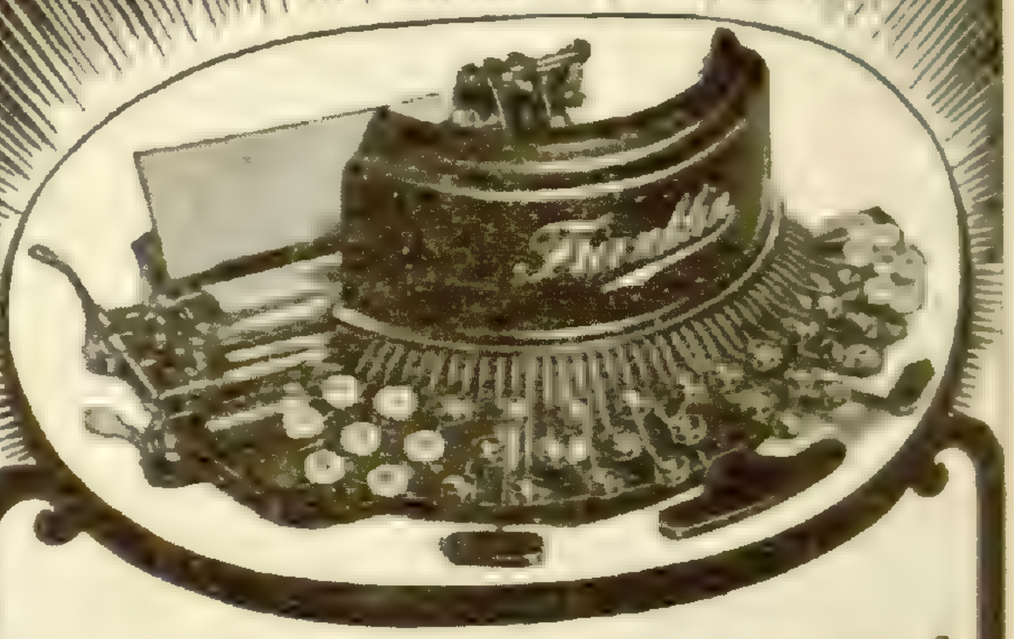

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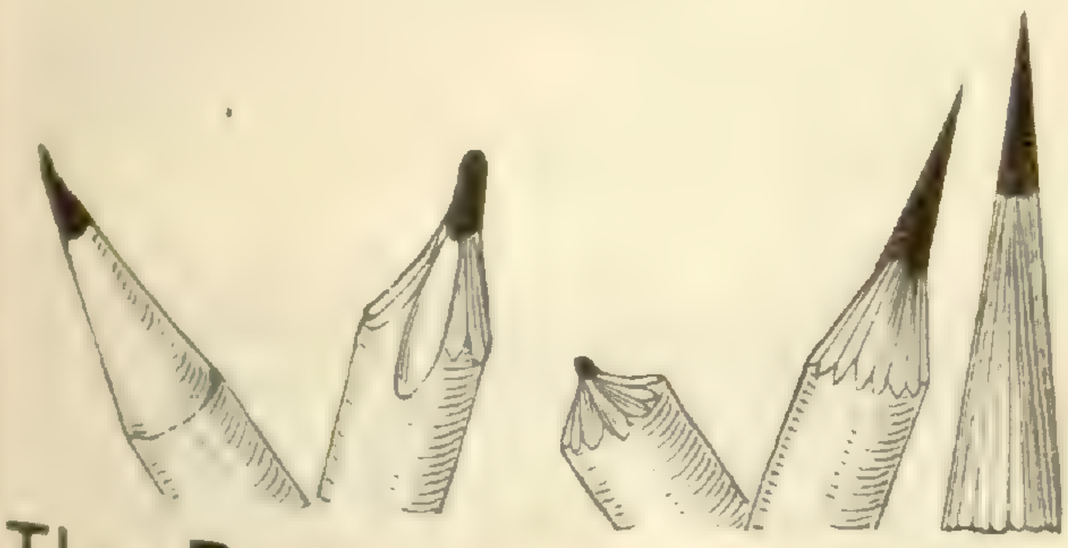

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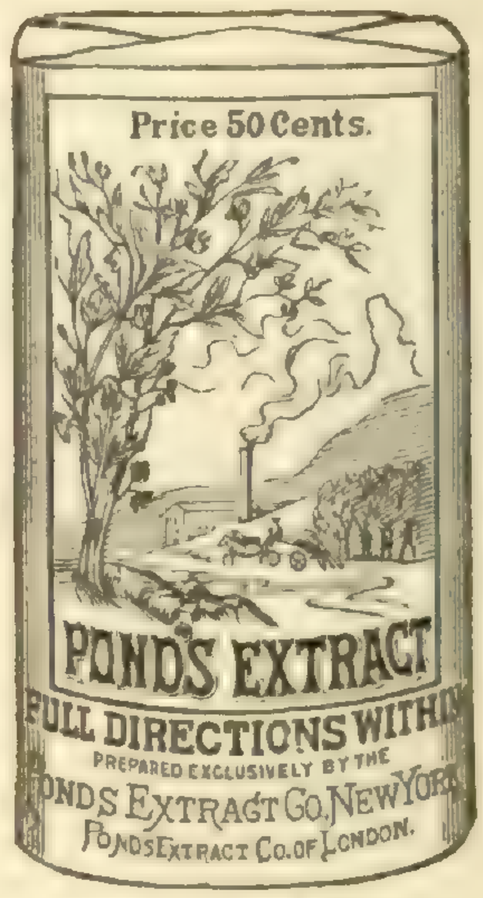

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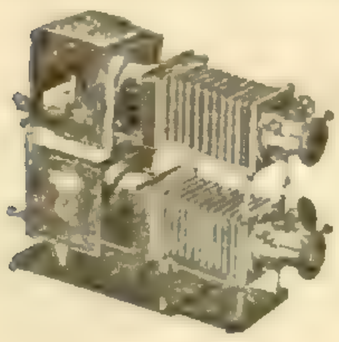

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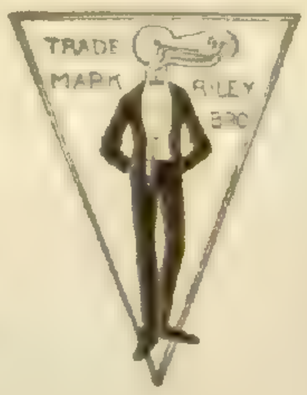

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VOLUME XXIX NUMBER 6

BOTANICAL GAZETTE

JUNE, 1900

BOTRYTIS AND SCLEROTINIA: THEIR RELATION TO CERTAIN PLANT DISEASES AND TO EACH OTHER.

RALPH E. SMITH.

(WITH PLATES XXV–XXVII AND THREE FIGURES)

IN connection with the work of the Hatch Experiment Station of the Massachusetts Agricultural College, a disease of hothouse lettuce has been under investigation for several years. The practical results of this investigation will appear in a bulletin of the station. It is the purpose of the present article to present some results of this study which seem to have a value beyond that of their practical relation to the lettuce disease, and to discuss these results, together with some obtained by other investigators, with a view to clearing up some unsettled points in the life history of certain fungi.

The question of the relation of certain species of the Polyactis section of the genus Botrytis to certain species of Sclerotinia is no new one. The literature of plant diseases, especially in Europe, abounds in descriptions and discussions of cases of plant diseases where one or the other or both of these forms appeared, and considerable difference of opinion has resulted as to their real relations to the disease and to each other. In this contention are involved principally two species of Sclerotinia, namely: *S. Fuckeliana* De By. and *S. Libertiana* Fckl., and one species of Botrytis, *B. cinerea* Pers. (*B. vulgaris* Fr., and numerous other synonyms). Largely on the authority of De Bary,

Botrytis cinerea has been considered the conidial form of *Sclerotinia Fuckeliana*, and the existence of any such conidial form of *S. Libertiana* has been denied. Some investigators have disputed this, however, claiming that in certain cases *Botrytis cinerea* has developed in undoubted connection with *Sclerotinia Libertiana*, thus casting doubts on the distinctness of *S. Fuckeliana*. The present article contains a description of the investigation of the above mentioned lettuce disease, in so far as it bears on this subject, together with some other observations made by the writer, and abstracts of descriptions of several similar diseases investigated by others.

1. The lettuce disease.

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In the Report of the Massachusetts Experiment Station for

1891 Humphrey (1) described a disease of greenhouse lettuce, from which the following is an abstract:

The trouble ordinarily appears first upon the stem of the plant, about at the surface of the soil. Here may be seen at first a soft, dark, decayed spot, which rapidly spreads, penetrating the stem and involving next the bases of the lower leaves. The latter, being thus cut off from the plant by the decay of their bases, usually dry up. With the further progress of the decay the center of the head, with the tender inner leaves, becomes attacked, and soon collapses into a fetid, slimy mass. In the decaying tissue one can often recognize fungus threads, and if they are left undisturbed, there appear on the decayed remains the fruiting threads and spores of a fungus; always the same. . . . . The fungus in question is one of the imperfect forms known as Botrytis or Polyactis. . . . . In its development, so far as observed, and in the details of its structure, this fungus appears to agree with the form known as *Botrytis* (*Polyactis*) *vulgaris* Fr.; and is with little doubt the conidial stage of some sclerotium-producing Peziza (Sclerotinia).

Since the above was written the lettuce-forcing industry in the vicinity of Boston has largely increased, and forms today one of the most important agricultural industries in the state. Diseases of the crop have naturally increased proportionally. It is evident that the trouble described by Humphrey covers what is now generally known in the lettuce district as the "drop," and probably also more or less of another disease distinguished by the growers as "black root." The "drop" is the worst obstacle to lettuce growing in the Boston district. Its general nature is described in the quotation from Humphrey. Plants growing finely and approaching maturity suddenly collapse, the stem at the surface of the ground and the bases of the leaves are found to be rotted, and in a day or two the plant is completely gone. Plants afflicted with the real "drop" never recover. In most of these sudden cases, however, no black spot appears on the stem as described by Humphrey, nor does any external change in appearance take place except that a white, mould-like fungus mycelium usually appears and grows vigorously upon the surrounding soil. This Humphrey does not mention, though it seems probable that he would have done so if it had occurred in the cases observed by him, as it is very striking. Careful study of these diseases show that many cases of "black root" come

closer to Humphrey's description. This trouble appears to start in some injury to the plant, such as the breaking off of a leaf, or where the plants grow poorly and the outer leaves die off. Starting in some such way a fungus growth develops which gradually works down into the stem on the side from which it started, producing a black, decayed spot, just as described by Humphrey. A growth of Botrytis appears on the affected parts, but the vigorous growth on the soil does not appear. The ultimate fate of such plants depends largely on the management of the greenhouse. If the soil is kept dry and the temperature low no great loss results, but should a period of high temperature and considerable moisture occur the plants soon "drop" in the characteristic manner. A trouble of this sort appears to be common wherever hothouse lettuce is grown. It has generally been ascribed to *Botrytis vulgaris*, largely on Humphrey's authority, and the idea appears to be general that it can be held in check by proper handling of water and ventilation. Thus Humphrey says:

> It is evident that the thorough and careful culture and vigilant supervision of the plants are essential to the control of the disease in question . . . . with a crop well nourished and well cared for one may legitimately expect practical freedom from loss by rotting.

The "lettuce rot" described by Jones (2) does not appear to be the "drop," although ascribed to *Botrytis vulgaris*. The trouble described by Taft (3) as caused by *B. vulgaris* may include the "drop," but the name "mildew" is ill-chosen. Galloway (4), referring to the Boston soil, says:

> Wet rot of the lower leaves and rotting of the stems and consequent wilting of the plant are seldom troublesome in this soil if properly handled, because the surface is at all times comparatively dry. Wet rot is produced by *Botrytis vulgaris*.

Bailey (6) has the same idea when he says:

> This lettuce rot is due to a fungus (*Botrytis vulgaris*) which lives upon decaying matter on the soil, but when the house is kept too warm and damp, and the lettuce becomes flabby, it invades the plant and causes irreparable damage. There is no remedy, but if the soil is sandy and "sweet" and the

house properly managed as to moisture and temperature, and top dressings of manure are avoided, the disease need not be feared.

Bailey's illustration shows a typical case of "drop." If these statements are to be believed the condition of affairs in many lettuce houses about Boston can but reflect seriously on the skill of their owners. The disease is there and in abundance, to all appearances the same trouble as described by Humphrey, Galloway, and Bailey. In some houses it is much worse than in others but the fact is undeniable that even in the houses of some of the best growers, men who possess a practical knowledge of their special crop second to none, the disease is almost unchecked. Evidently, therefore, *Botrytis vulgaris* is a more serious parasite than is generally supposed, or else some other organism or agency is at work, producing a similar effect.

The first cases of the disease examined by the writer agreed very well with Humphrey's description. The plants were completely collapsed and the stems and bases of the leaves soft and rotten. The affected tissue was filled with a vigorous mycelium (*fig. 51*). This mycelium was composed of large, branching, septate, hyaline filaments, filled with granular protoplasm, but with numerous vacuoles in the older portions. The larger filaments averaged about 13μ in diameter. On the borders of affected tissue filaments could be seen advancing (*fig. 50*). When placed in a moist chamber over night, the plants became covered in the affected parts with a vigorous growth of the conidial form, *Botrytis vulgaris* Fr. This growth, to all appearances, originated directly in the parasitic mycelium which had destroyed the plant. The conidiophores developed from the interior filaments (*figs. 13–17*). *Fig. 18* shows the development of the branches, and *figs. 1* and *2* represent a typical conidiophore of this species. The peculiar branching forms known as "organs of attachment" (*figs. 19–26*) were also abundantly produced from the mycelium on affected plants and in cultures, which could readily be made on prune juice, prune bread, prune gelatine or agar, boiled fruits or vegetables, or almost any nutrient substance. Contrary to Humphrey's results, sclerotia

were produced abundantly on affected plants and in cultures. These were very small and insignificant, but numerous in every case.

Humphrey's conclusions that the disease is caused by *Botrytis vulgaris* appears to have been generally accepted by all who have written concerning this disease. It is very probable that in some of the citations given above the disease was not the real stem rot or "drop," but simply a case of Botrytis on the leaves, as often occurs on all kinds of plants when growing poorly or under unfavorable conditions. But in many of the references it is evident that the typical stem rot was found and ascribed to Botrytis. In no case was any extended investigation made. Early in the writer's study of this disease it became evident that whatever the cause might be, many cases occurred in which no Botrytis could be found, although otherwise the disease was very typical. Extended observation of a very large amount and variety of material from various sources has shown the existence of what may be called three forms of the typical disease. This excludes some other lettuce troubles of a more or less similar nature.

THE BOTRYTIS TYPE.

This form of the disease has already been described in a general way. It should be clearly distinguished from cases where Botrytis grows locally, more or less as a saprophyte, or even as a true parasite, upon the outer leaves. The rotting of the stem and collapse of the leaves and head is the characteristic of this and all types of the real "drop." *Botrytis vulgaris* is well known as one of the fungi, though not, perhaps, the most common, which cause the death of young seedlings and cuttings by what is known as "damping off," a trouble entirely similar to the "drop" in its effect, being a rotting of the stem at the surface of the ground. The principal difference between "damping off" and "drop" from a practical standpoint is in the age of the plants affected. "Damping off" of lettuce seedlings is common and may often be traced to Botrytis. It would not

seem remarkable, therefore, for so similar a disease as the "drop" to be caused by the same fungus. But of course the occurrence of this so common species upon affected plants comes far from proving it to be the parasite, and especially since many cases of the typical disease occur where no trace whatever of this fungus, or at least of its conidial form, can be found, Humphrey's conclusions cannot be accepted without further and more definite proof. The most convincing case in this respect seen by the writer was that of a crop of lettuce grown in one of the station greenhouses in the winter of 1898–9. The "drop" had been introduced into this house for purposes of study in 1897 and had been abundant in each crop since then. In no case, however, had any Botrytis appeared. Meantime, a method of treatment had been developed by which this no-botrytis type of the disease was completely held in check. The treatment consisted in sterilizing the soil by means of steam, and crop after crop was grown, with or without the disease at will. When this crop was set out the plants were overgrown and "spindling," having been too long in the flats. Consequently the outer leaves died off and the plants received a severe set back. Added to this the house was not properly ventilated and on several occasions the temperature was much too high. Soon after being set out the plants began to "drop," and in a few weeks the majority of them, in treated and untreated soil alike, were gone. Affected plants showed a mycelium in the stem indistinguishable from that in all other cases. Organs of attachment occurred as usual. Botrytis was abundant on every plant, especially when kept over night in a moist chamber. No mycelium was visible upon the surface of affected plants nor did it spread to the surrounding soil, and it could not be seen that the disease spread from plant to plant. The leaves were scarcely or not at all affected except at the very base and the rotting was almost entirely confined to the stem, the rest of the plant drying up. There is no reason to doubt that these plants were affected primarily with *Botrytis vulgaris*, originating presumably from conidia in the air, and such is believed to have been the case. It appeared to be essentially a

case of belated "damping off," made possible by the weakened condition of the plants.

Cultures made from affected tissue from these plants and from the Botrytis conidia gave similar results. A rather scanty mycelium developed, bearing numerous organs of attachment and but few conidia. Often no spores developed until after several weeks, even in cultures made directly from conidia. Compared with cultures made from ordinary saprophytic *Botrytis vulgaris*, these seemed to show that as the fungus takes on a parasitic nature it produces fewer conidia and more organs of attachment, though it is extremely variable and uncertain in these respects. Sclerotia were sparingly produced in almost all cultures made from this material. These appeared first as reddish, blister-like elevations in the substratum, gradually becoming black and hard. They were mostly longer than broad, thin, firmly attached to the substratum and inseparable from it. *Text fig. 1 f* shows some of these sclerotia grown on gelatine, portions of which are still attached to them. The photograph does not bring out clearly the size and form of the single specimens, as it is impossible to separate them cleanly. Thus, *text fig. 1 f*^{a} is a piece of gelatine having on its surface two long, thin, narrow sclerotia lying parallel to one another, while *f*^{b} consists of several sclerotia with more or less gelatine. *Fig. 44* also represents some of these forms, but fails to bring out their thinness. If placed in wet sand soon after being formed these sclerotia produced an abundant crop of Botrytis conidiophores and conidia. The ability to produce conidia appeared to be lost with age, and after a few months drying the development was largely of mycelium, though this was rather scanty.

In order to determine still more fully the relation of Botrytis to the lettuce disease some investigations were made along the line of infection experiments. Humphrey reports such to have been unsuccessful. Experiments on early mature lettuce plants gave the following results.

1. Pieces of affected plants buried in the soil beside healthy plants generally produced the disease.

2. Diseased plants from the lot just described, which appeared to have a pure Botrytis disease, did not have this effect.
3. Water containing abundant conidia poured down into the head produced no effect.
4. The same result was obtained when the leaf stalks were

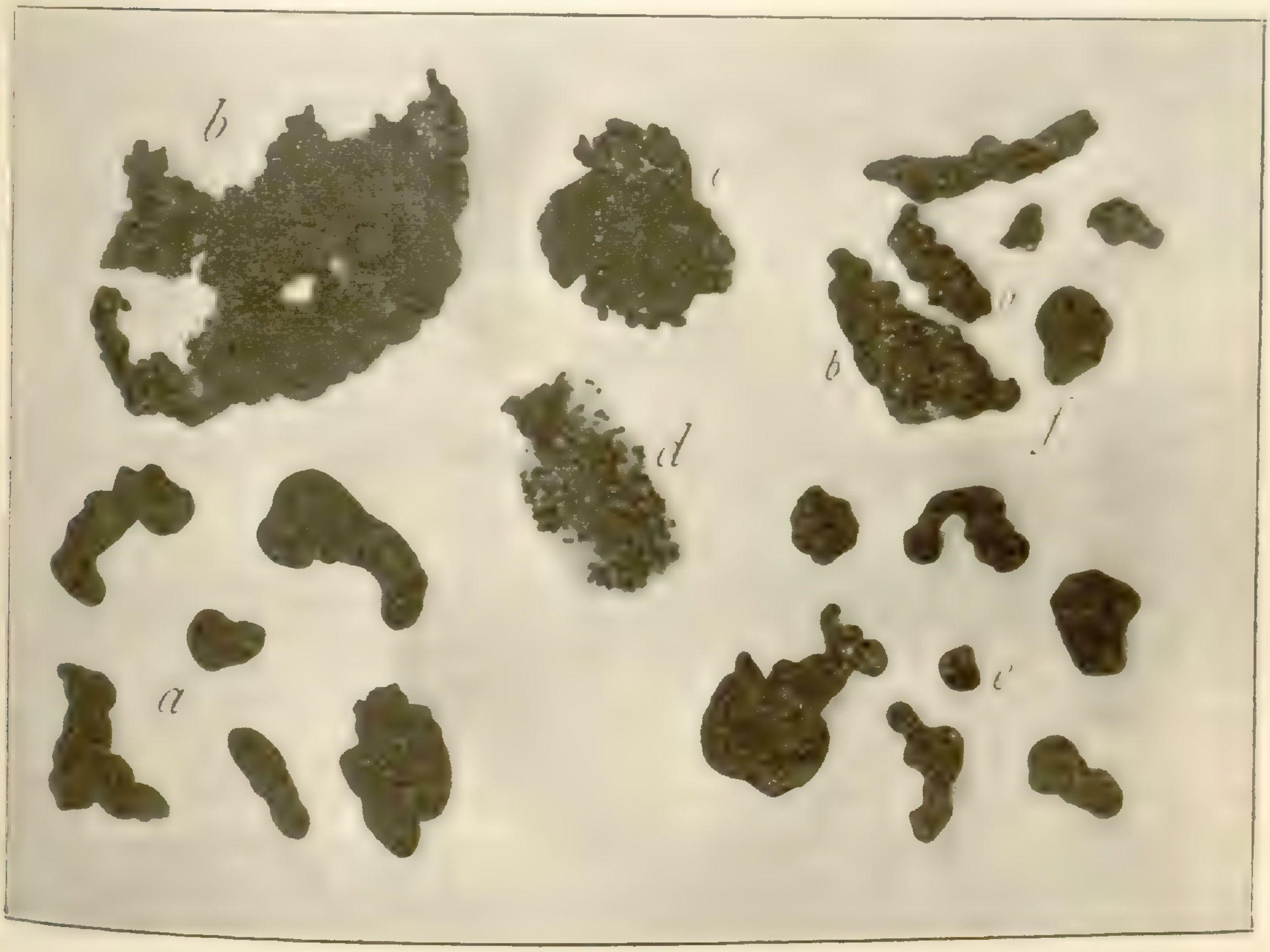

FIG. 1.—*a*, sclerotia of *Sclerotinia Libertiana*: *b*, *c*, sclerotial crust of lettuce fungus; *d*, small sclerotia from lettuce fungus; *e*, sclerotia of *S. Libertiana* from alfalfa; *f*, sclerotia of *Botrytis cinerea*.

cut into so that the conidia came into contact with wounded tissue.

5. Conidia dusted all over plants in great abundance had no effect.
6. Plants treated as in 5 but covered with a bell jar became affected in the leaves, which gradually died and rotted away, but the stem was unaffected and no typical "drop" resulted.

7. When the stem was cut into at the surface of the ground and mycelium and conidia inserted, no effect was apparent.

From these experiments it appears that the typical "drop" cannot be produced from Botrytis conidia in vigorous lettuce plants under ordinary conditions.

The following experiments were made with lettuce seedlings. A dish of soil was sterilized and then thoroughly inoculated with fresh Botrytis conidia. Lettuce seed was then sown. The plants came up well and remained entirely unaffected. The soil was then sprinkled heavily with conidia among the seedlings, with the result that one "damped off." The stem was permeated with a mycelium entirely similar in appearance to that found in the "drop." A portion of this is shown in *fig. 27* (cf. *fig. 51*).

The dish was then covered with a bell jar and kept very moist, but no more plants were affected. Prune juice containing conidia was then poured amongst the plants and the dish kept in the open air. "Damping" at once set in, and in a few days all the plants succumbed in the characteristic manner. Cultures made from these plants on prune and turnip showed the parasitic peculiarities of Botrytis already referred to. A considerable mycelium was produced at first but very few conidia until later. Raw turnip was readily attacked and caused to rot. This experiment corroborates Kissling's[1] results in regard to *Botrytis cinerea* that conidia are unable to, or at least do not readily, attack living tissue except after previous saprophytic nourishment.

In respect to the general question as to the relation of Botrytis to the "drop," these results seem to show that the disease is not produced in vigorous plants by direct infection from conidia in the air or soil, although in the case described above, where the vitality of the plants was very low, such appears to have been the case. The same conclusion may be deduced from the usually sucessful result of sterilizing the soil. There appears to be no doubt that the cases where "black root" develops into the "drop" belong to this form of the disease, and also the trouble which Humphrey, Galloway, and Bailey had in mind in referring

[1] Hedwigia **28**: 227. 1889.

to its treatment. Were this the only form to occur it would cause little trouble in the Boston district, as it is almost unknown there except for an occasional case of "black root."

THE NO-BOTRYTIS TYPE.

Among all the cases of the disease examined by the writer, those in which Botrytis appeared have been by far the exception. In the type of the disease most prevalent in Massachusetts no conidial form whatever can be found. In its general effect the disease is entirely similar to that already described and indistinguishable from it. Affected plants wilt and collapse and in a few days are entirely destroyed. The usual mycelium is found in the stem. It is also usual to find an abundant, white, woolly mycelium proceeding from affected plants to the surrounding soil where it flourishes luxuriantly for a time, often spreading to and attacking adjacent plants. In fact it is evident that whatever form of reproduction this fungus may possess its principal mode of spreading in the greenhouse is by growth in the soil. Wherever one plant is attacked the neighboring ones almost always follow, and the mycelium grows luxuriantly upon the soil, extending from plant to plant. On coming into contact with a healthy leaf it spreads over the surface, forming numerous organs of attachment (*fig. 31*). *Fig. 29* shows in cross section the result of this, the epidermis breaking down and the filaments penetrating and destroying the leaf. Sclerotia are formed in considerable abundance on affected plants, especially on the stem and beneath the leaves, but they are very small and easily overlooked in the soil. Cultures are easily made with bits of affected tissue or mycelium, and hundreds have been made in this way with no sign of Botrytis. Such cultures produce a considerable mycelium, more abundant on bread than on gelatine, and very numerous sclerotia. This mycelium is composed of filaments indistinguishable from those in the botrytis form. Organs of attachment are numerous and entirely similar. The sclerotia are very small, mostly about the size of a pin head. Some are a little larger, but thin and irregular in shape, while often a sort

of black sclerotial crust is formed, an inch or more in diameter, but not much thicker than paper. *Fig. 42* and *text fig. 1 d* show the small sclerotia of this type, and the crust-like growth is shown by *text fig. 1 b* and *c*, and by *fig. 43*. A clear distinction can be seen between the formation of sclerotia in this and in the botrytis form. Here they first appear as white specks in the mycelium, gradually becoming black and hard. They are not as long as those of the other form, and lack entirely the very characteristic blister-like connection with the substratum, being entirely distinct from it and imbedded in the mycelium. They are also produced much more abundantly. Many trials were made to obtain further development from these sclerotia. When placed on moist sand they usually produced a growth of mycelium, more copious from old specimens than fresh ones. Old dry material a year old grows luxuriantly when kept moist for a few days, producing much more mycelium than the Botrytis sclerotia. What might be called secondary sclerotia are also produced on such growths. On the surface of clean sand, on moist filter paper, or even on the bare bottom of a glass dish, when kept covered and moist, the mycelium coming from a sclerotium produces often a considerable number of smaller ones. The same result is often seen when a piece of affected tissue is placed in a moist chamber (*fig. 45*); and upon the surface of the soil about, and especially beneath the leaves of the affected plants, such secondary sclerotia are commonly produced. Being so small, however, they are difficult to distinguish in the latter case. Other than this no development has been obtained from these sclerotia except in one case. One of the largest specimens, about 3^{mm} in diameter, after being in the sand for some time, threw up a slender stalk (*fig. 35*). This reached a height of nearly 1^{cm}, but then withered and faded away without attaining any farther development.

Since no reproductive structures of this form could be obtained, infection experiments were only possible by using diseased tissue or masses of mycelium as infective material. Such experiments were almost invariably successful. Using plants

which showed this type of the disease in its purest form, or cultures made from them, it was found that when bits of diseased tissue were buried in the soil beside healthy plants, or inserted in cuts in the stem, the disease was at once produced. It was further found that if affected plants or portions of them were buried in a flower pot and lettuce plants set in, the latter would soon begin to die off and all eventually succumb, the mycelium soon appearing upon the surface of the soil in the characteristic manner. With sclerotia, pure mycelium, or pieces of sclerotia, the same results are obtained. In none of the experiments were the plants covered or placed under any conditions different from those of ordinary greenhouse culture. These results show plainly that this species or form is an active parasite, capable of causing the disease in the most vigorous plants at any age, but at the same time able to flourish under purely saprophytic conditions. It is likewise able to reproduce itself from year to year indefinitely by purely vegetative development, forming freely, either as a saprophyte or parasite, sclerotia which are able to survive all ordinary conditions[2] and produce the fungus anew. It would seem, in fact, that this is the only method of reproduction of this form. The results of sterilizing the soil have been already alluded to. It was found that when not less than three inches of the surface soil had been steam sterilized not a plant was affected, even in the worst infested beds. The only exception to this was the one crop where the pure botrytis type occurred. Plainly, therefore, the no-botrytis form depends very largely, if not entirely, upon saprophytic growth in the soil and the sclerotial resting stage for the continuance of its existence.

THE LARGE SCLEROTIA TYPE.

In a lot of lettuce plants sent by a gardener in eastern Massachusetts a third type of the "drop" was found. In this case the general nature of the disease was typical, and the parasitic

[2] Many results that relate to the biology of these forms are omitted here as they do not bear on the present subject.

mycelium indistinguishable from that found in other cases. No Botrytis appeared. The peculiarity of this form was that the sclerotia which were rather sparingly produced on the plants, were quite large and thick, much more so than in the ordinary no-botrytis type. In cultures numerous large, well-formed sclerotia appeared, some being an inch long and thick and solid (*fig. 41*, and *text fig. 1 a*). These sclerotia could be grown by the quart on suitable media, dishes of prune bread being especially favorable. Their development is similar to that of the smaller ones in the last type described. Beginning as a white, harder spot in the mycelium they gradually enlarge, becoming, when mature, black and hard. They have no connection with the substratum, being imbedded in the mycelium and easily separated from it. During their formation drops of a clear liquid usually appear on the surface, and in old cultures the sclerotia and mycelium often become incrusted with rod-shaped crystals of calcium oxalate. In cultures and on diseased plants organs of attachment are very abundant and entirely similar to those already mentioned.

FIG. 2.—Sclerotia and apothecia of *Sclerotinia Libertiana*; slightly reduced.

When placed on wet sand these sclerotia soon began to throw up slender stalks, usually several from each, which expand into trumpet-shaped Peziza apothecia. These bodies varied somewhat in size and shape, as shown by the typical forms in *text fig. 2*.

The disks have the usual discomycetous structure as shown in section (*fig. 32*). Asci and paraphyses are shown more enlarged in *fig. 33*. This fungus was a typical form of *Sclerotinia Libertiana* Fckl. (*Peziza Sclerotiorum* Lib., etc.)

Similar infection experiments to those in the last case made with this material gave the same results. Diseased tissue or portions of mycelium never failed to produce the disease in healthy plants. No experiments have been made with ascospores in respect to infection. The conclusion is a safe one that *Sclerotinia Libertiana* is an active parasite of lettuce and, in some cases at least, the cause of the disease under consideration. The form just described, however, is far from common in greenhouses, and certainly does not occur in the great majority of cases of the "drop".

GENERAL CONSIDERATION OF THE CAUSE OF THE DISEASE.

These three types cover all the cases of the disease which have been seen by the writer. The last occurred in but a single lot of plants. The second represents the bulk of the disease in this state. The first in its purest form was found only in the single lot of plants described and occasionally in a few plants in a crop soon after setting. Cases are not rare, however, which appear to be a mixture of the first and second. Botrytis develops on affected plants but cultures from the most newly affected inner tissue give no Botrytis but characteristic growth of the no-botrytis form.

The observations thus far recorded are sufficient to establish the following statements:

The "drop," in the majority of cases, is a strictly parasitic disease and attacks the most vigorous plants.

The ordinary Botrytis in its conidial form does not cause the disease except in exceptional instances.

Either of the last two forms described is able to cause the disease in a strictly parasitic manner.

The disease is spread and infection takes place most commonly by saprophytic growth through the soil.

The fungus which causes most cases of the disease is able to exist indefinitely in the soil by means of sclerotia, which may be formed either upon affected plants or by purely saprophytic growth in the soil and appear to form the usual, if not the only, mode of reproduction.

This fungus may be exterminated by heating the soil.

In exceptional cases the "drop" appears to have been caused by the conidial form of *Botrytis vulgaris*, but only in plants which were under unfavorable conditions.

The disease may be caused by a typical form of *Sclerotinia Libertiana* Fckl., but this is exceptional.

In all cases of the disease there is the closest resemblance in the effect on the plant and in the parasitic mycelium which attacks it, the latter applying to the filaments and the organs of attachment which they bear.

The most marked differences between the three forms are found in the production of Botrytis conidia in the first and its absence in the other two; in the production of the Peziza stage in the last; in the form and size of the sclerotia and the manner of their production; and in the general greater development of the mycelium and its spread over the soil in the last two types.

On the basis of these statements the following suppositions are possible as to the relations of these forms to one another and the real cause or causes of the disease.

1. The three types are caused by three distinct species of fungi which are peculiarly coincident in certain respects.

2. The three types are caused by three different forms of the same species, which accounts for the coincidences.

3. Two of the forms belong to the same species while the third is distinct but similar in certain respects.

CULTURES.

In order to test further these hypotheses a large number of special cultures were made which may now be described. The specific object of these experiments was to find out, by growing the three forms of fungi under various conditions, whether any

of the forms could be changed into any other, or to prove definitely that they are all distinct. To accomplish the former required that Botrytis be developed in a pure culture of one or both of the no-botrytis forms, that one or both of the typical no-botrytis forms be developed from Botrytis conidia, or that the typical *Sclerotinia Libertiana* be developed from the ordinary no-botrytis form or *vice versa*.

Growth on various media.—Cultures of the three forms were made on a considerable variety of substances to test their effect on the organisms. These substances included various fruit decoctions, bread soaked with various nutrient juices and decoctions, and boiled fruits and vegetables of many different kinds. A detailed account of these cultures is unnecessary as in every case the growth was typical of the original material and no marked changes appeared.

Effect of low temperature.—Here again no results were obtained. It was found that each of the forms, with proper nourishment, continued to grow almost down to the freezing point, but naturally with much less vigor at the lower temperatures. No other effect than this was observable with the no-botrytis forms. With Botrytis no conidia developed in cultures kept below 5° C., a feeble mycelium being the only growth. When put in a warm place, however, these cultures at once grew in the ordinary manner, producing abundant conidia.

Effect of darkness.—No marked effect was produced by growth in total darkness.

Effect of starvation.—Cultures made in pure gelatine with no nutrient addition showed nothing more marked than a feeble growth.

Effect of solidity of substratum.—This was tested by using nutrient agar of different degrees of solidity. Growth was not as vigorous upon the hardest grades, but no other effect appeared.

Effect of acid and alkaline media.—These experiments were made by using as a nutrient medium prune juice of different degrees of acidity and alkalinity. The decoction was first carefully neutralized by an experienced chemist, using sodium

hydrate and tartaric acid weighed out in the dry form and added to the prune juice in the proper amounts; the following series of flasks were made up: $\frac{1}{10}$, $\frac{1}{2}$, 1, 2, 3, 4, 5, and 10 per cent. acid, with similar alkaline series.

With Botrytis no results affecting the main question were obtained from these cultures. After four days good mycelium and conidia had developed in alk. $\frac{1}{10}$ per cent., neutral, and $\frac{1}{10}$, $\frac{1}{2}$, and 1 per cent. acid. Acid 2 per cent. had considerable mycelium, rather dense, and a few conidiophores. Acid 3, 4, and 5 per cent. had a smaller amount of dense mycelium, forming a compact membrane. Acid 10 per cent. had merest trace of development. Alk. $\frac{1}{2}$ per cent. had good mycelium, loose and flocculent, with some conidiophores around the edges. Alk. 1 per cent. about the same but with very few conidiophores. Alk. 2 per cent. poorer mycelium with woolly, flocculent appearance and no conidia. Alk. 3 per cent. merest trace of development. Alk. 4, 5, and 10 per cent. no growth. Two weeks later conidia were abundant in all the acids except the 10 per cent., which showed no growth. The alkalies had quite abundant conidia below 3 per cent., but from there on very little or no development. Acid 1 per cent. gave about as vigorous and typical a Botrytis growth as any. The contrast was very marked between acid 2–5 per cent. and alk. 1–2 per cent. The former formed a close dense membrane, while the latter was loose, woolly, and flocculent. No particular difference in the filaments could be seen with the microscope. While these results have some little general interest they gave no evidence as to a connection between Botrytis and other "drop" fungi. The no-botrytis fungus with small sclerotia showed no such striking differences in development in acid and alkaline media as did Botrytis. Its range of growth was about the same and the effect upon the mycelium was somewhat similar but by no means as marked. From one culture of this sort, however, a valuable result was obtained. This was a large flask of prune of considerable alkalinity but not made up in definite proportions. It was inoculated with mycelium from a pure culture of the small-sclerotia fungus, coming

originally from lettuce in a house which had never contained any other form of the disease. In this culture the usual small sclerotia were first produced, but later there appeared a considerable number of larger ones, appearing similar to those of *S. Libertiana*. A number of these were obtained and cultures made from them on ordinary prune bread, with the result that the typical large-sclerotia type developed. No spores of this type had ever been developed in the laboratory at the time this culture was made nor had any trace of the large-sclerotia form ever appeared in connection with any of the material used, so that there would seem to have been no possible chance for accidental infection. Consequently the only possible explanation seems to be that *Sclerotinia Libertiana developed directly from the small-sclerotia, no-botrytis form.*[3] (In this connection should be borne in mind the fact already mentioned that in one case one of the small sclerotia started to develop an apothecium just as in *S. Libertiana*.)

CONCLUSIONS.

From all the observations and experiments thus far recorded it is concluded:

1. That the lettuce "drop" in Massachusetts is caused by two distinct species of fungi, namely, *Botrytis vulgaris* Fr. and *Sclerotinia Libertiana* Fckl., which are remarkably alike in some respects and have an entirely similar effect upon the plant.

2. That the bulk of the disease is caused by a degenerate form of the latter species, which has almost entirely lost the ability to reproduce by spores but which is highly specialized as a vegetative, facultative parasite.

3. That the disease is caused by *Botrytis vulgaris* and the typical *Sclerotinia Libertiana* in mature plants only in rare instances; the former on account of its inability to attack vigorous plants under normal conditions, the latter because of its infrequent occurrence.

[3] It is not asserted that this result is to be attributed to the alkalinity of the culture medium.

4. That in many cases Botrytis develops as a saprophyte on plants primarily affected by the other species and is mistaken for the true parasite on account of the similarity of the mycelium.

5. That these forms and species can be distinctly separated by means of pure cultures, and distinguished from one another by the form and manner of growth of the sclerotia.

NOTE.—No reference has thus far been made to the internal structure of the sclerotia. De Bary (Morph. and Physiol. p. 31) draws a distinction between the Botrytis and *Scl. Libertiana* forms on the basis of structure, but the writer has not been able to establish this or make a uniform distinction. *Fig. 39* shows a section which might represent any of the forms.

Thus it appears from the study of this disease that *Sclerotinia Libertiana* has no connection with the Botrytis form in question, although at first sight this appeared to be undoubtedly the case. Confusion has arisen from the similarity in the parasitic mycelium of the two forms, their similar effect on the plant and their frequent simultaneous occurrence; coincidences most deceptive to superficial examination but easily explained on the ground of the close relationship between the two species. Too general conclusions should not be drawn from the case of this disease, however, without taking into consideration a number of very similar ones which have been described. The writer has been fortunate in obtaining material of a number of these diseases, as well as additional information concerning some of them, and has spent considerable time in comparing them with the results obtained from the study of the lettuce disease. Careful inquiry shows at once that much has been taken for granted in many of these cases and conclusions drawn which were based more on apparent probability and general appearances than actual proof. It must be conceded that in a number of cases which are mentioned hereafter the conclusion seems at first sight fully warranted that *Botrytis cinerea* is a stage in the life history of *Sclerotinia Libertiana*, so intimately are the two forms associated with one another and so similar are they in effect and many details of structure. But, as will presently appear, in every case which the

writer has been able to investigate or obtain full information about, as well as from his general study of the species of fungi concerned, the conclusions based on the study of the lettuce disease are fully substantiated. Three classes may be made of the diseases of this nature as follows: (1) diseases where both *Sclerotinia Libertiana* and *Botrytis cinerea* (*vulgaris*, etc.) appeared; (2) diseases attributed to Botrytis alone; and (3) diseases attributed to Sclerotinia alone.

II. Diseases attributed to Sclerotinia and Botrytis.

As a type of this class, which would include the lettuce disease, may be taken the disease of hemp described by Behrens and others.

HEMP DISEASE.

BIBLIOGRAPHY.

1. TICHOMIROFF, W. *Peziza Kaufmanniana;* eine neue, aus Sclerotium stammende und auf Hanf schmarotzende Becherpilz-Spezies. Bull. Soc. Nat. de Moscou.—: 294. 1868.

2. HAZSLINSZKY, F. *Polyactis infestans.* Grev. 6: 77. 1877.

3. DE BARY, A. Ueber einige Sclerotinien und Sclerotinienkrankheiten. Bot. Ztg. 44: 378. 1886.

4. BEHRENS, J. Ueber das Auftreten des Hanfkrebses in Elsass. Zeitschr. f. Pflanzenkrankh. 1: 208. 1891.

5. SORAUER, P. (*a*) Die Schäden der einheimischen Kulturpflanzen. (Zeitschr. f. Pflanzenkrankh. 1: 212. 1891.)
(*b*) Hanfkrebs. Pflanzenkrankheiten 289.

6. HILTNER, L. Einige durch *Botrytis cinerea* erzeugte Krankheiten. Inaug. Diss. 1892.

7. FRANK, A. B. Sclerotienkrankheit des Hanfes. Die Pilzparasitären Krankheiten der Pflanzen 499.

A disease very similar to that of the lettuce is described by Behrens (4) on hemp. For several successive seasons a stem rot of this plant was observed in Alsace. Affected stems were permeated with large, intercellular filaments, while upon the surface appeared sclerotia resembling the old form *Sclerotium varium*. In the interior cavity of the stem were also numerous sclerotia. Upon some affected plants a growth of *Botrytis cinerea* appeared,

the mycelium of which agreed entirely with that in the stem. In a moist chamber Botrytis appeared on many of the plants. Material received the following year showed no trace of Botrytis; otherwise the disease was exactly the same. Cultivated on bread the fungus produced abundant sclerotia but no Botrytis, while in the previous year the conidial form appeared in cultures regularly. The author concludes that the organism is similar to *Sclerotinia Libertiana* in every way except for the Botrytis conidia, which form is supposed to characterize *S. Fuckeliana*, and states that one of two cases is possible; either the Botrytis is secondary on stems affected primarily with *S. Libertiana*, or else the fungus occurs varyingly, with or without Botrytis conidia. The results of inoculation experiments with Botrytis conidia appeared to support the latter hypothesis, that the Sclerotinia may appear with or without Botrytis. Whether it should be called Fuckeliana or Libertiana the author was unable to decide.

Some time after the above was published, in the spring of 1898, the writer visited Dr. Behrens at Karlsruhe and was informed by him in regard to this disease that after more extended observation and consideration he inclined to the opinion the Botrytis and Sclerotinia might after all have been distinct species on the hemp, having no connection with one another.

Tichomiroff (1) found a disease of hemp in Russia with which that described by Behrens appears to be identical. He observed numerous sclerotia and named the form *Peziza Kaufmanniana*. No mention is made of a Botrytis stage. De Bary (3) found it possible to infect hemp with ascospores of *Sclerotinia Libertiana* and decided that *Kaufmanniana* was the same species.

Hazslinszky (2) found a fungus parasitic on hemp in Hungary which he named *Polyactis* (*Botrytis*) *infestans*. Behrens considered this as probably a form of *B. cinerea*, although the conidiophores, as figured by Hazslinszky, are articulated in a peculiar manner.

Hiltner (6) found a hemp disease with symptoms agreeing with those described by Behrens, Tichomiroff, and Hazslinszky, wherein no sclerotia appeared but abundant *Botrytis cinerea*.

The writer was unable to obtain material of this disease and consequently has no original information to offer concerning it. This case has been brought forward as one of the best examples of the connection between Botrytis and *Scl. Libertiana*, but Dr. Behrens' later statement changes the aspect completely. With his original conclusions discredited by himself there remains the fact that Tichomiroff and Hiltner found the disease caused respectively by Sclerotinia and Botrytis alone, and no proof is to be found that the two forms had any connection with one another in attacking this plant. The fact that Behrens found no Botrytis in connection with the disease during one season gives further evidence that this species was entirely distinct, though in similar effect and appearance.

RAPE DISEASE.

BIBLIOGRAPHY.

1. HAMBURG, E. A. *Peziza ciborioides* Fr., etc. III. Földniv. Erdec. 8:509. 1880. (Bot. Centralb. 8 : 172. 1881.)

2. DE BARY, A. *loc. cit.* 458.

3. FRANK, A. B. Sclerotienkrankheit des Rapses. *loc. cit.* 493.

4. SORAUER, P. Die Sclerotienkrankheit des Rapses. *loc. cit.* 297

The disease of the rape plant described by Frank (3) is also one of interest in this connection. Plants were found to be affected by a rotting of the stem, the cortex and pith being filled with a fungous mycelium, soon becoming completely destroyed. Numerous black sclerotia were present in the pith cavity. The filaments of the mycelium were hyaline, filled with granular protoplasm with vacuoles, septate and branching profusely in all directions. The largest had a diameter of 20μ. The sclerotia were of irregular form and had a diameter of $2–10^{mm}$. In places where the plants stood close together *Botrytis cinerea* often appeared upon the diseased portion of the stem. When affected stems were put under conditions of moisture this always occurred. The Botrytis hyphae seemed to arise without doubt from the interior filaments. Further development was obtained by placing sclerotia on moist sand, when they produced

apothecia, which the author attributes to *Sclerotinia Libertiana*. It was found possible to infect healthy rape plants with either conidia, ascospores, or mycelium, or by sowing the seed in a pot of earth containing diseased tissue. Seedlings were infected with Botrytis conidia and kept under a bell jar. They soon showed the disease as before. The author also cites the results obtained by Hamburg (1), who found it possible to infect healthy rape plants with ascospores of *S. Libertiana*, producing the disease with a development of Botrytis conidia, and he (Frank) concludes that the distinction of the two species *S. Libertiana* and *Fuckeliana* on the basis of presence or absence of the Botrytis form is impossible.

De Bary (2) discredits Frank's conclusions as to the connection between *S. Libertiana* and Botrytis.

This case seems to be the strongest argument in support of the connection between Botrytis and *Scl. Libertiana*. The writer has no personal knowledge of the disease. It should be pointed out, however, that Frank's results are really but little different from those obtained in the study of the lettuce disease where opposite conclusions were reached. The principal evidence in favor of the connection between the two forms is based on their simultaneous occurrence and the fact that the disease was induced in healthy seedlings kept under a bell jar by infection with Botrytis conidia, both of which facts apply equally well to the lettuce disease as already described. Nor are Hamburg's results any more convincing, since the appearance of Botrytis as a saprophyte on plants attacked by Sclerotinia is no unusual occurrence. The appearance of Sclerotinia (meaning sclerotia capable of producing Peziza) upon plants infected with Botrytis conidia would have carried great weight, but no such result has been obtained. The writer feels justified in stating in regard to this disease, on the testimony of those who have described it, and in the light of the similar cases which he has investigated and the general study of the species concerned, that no positive proof whatever is found herein that *Botrytis cinerea* and *Sclerotinia Libertiana* have any connection with each other.

POTATO DISEASE.

BIBLIOGRAPHY.

1. SMITH, W. G. (*a*) New form of disease in potatoes. Gard. Chron. N. S. **14** : 264. 1880.

(*b*) Disease of potatoes. Nature **28** : 299. 1883.

(*c*) New disease of potatoes. Diseases of field and garden crops 15.

2. Nature **28** : 231. 1883.

3. WILSON, A. S. (*a*) Disease of potatoes. Nature **28** : 343. 1883.

(*b*) Potato disease. Gard. Chron. N. S. **20** : 333. 1883.

4. BLYTT, A. Disease of potatoes. Nature **28** : 367. 1883.

5. DE BARY, A. *Loc. cit.* 436.

6. COHN, F. Illustr. landw. Ztg. 1887.

7. KIRCHNER, O. Die Stengelfäule, eine neue auftretende Krankheit der Kartoffeln. Würmtembergisches Wochenblatt für Landwirtschaft **30** :—. 1893.

8. RITZEMA BOS, J. (*a*) Kurze Mittheilungen über Pflanzenkrankheiten und Beschädigungen in den Niederlanden in den Jahren 1892 und 1893. Zeitschr. f. Pflanzenkrankh. **4** : 144. 1894.

(*b*) Kurze Mittheilungen, etc., im Jahr 1894. Zeitschr. f. Pflanzenkrankh. **5** : 286. 1895.

9. SORAUER, P., Editor. Einige Notizen über die in den letzten Jahren in Deutschland aufgetretenen Krankheitserscheinungen. Zeitschr. f. Pflanzenkrankh. **5** : 97. 1895.

10. REHM, H. Ascomyceten. Rabenhorst's Kryptogamen Flora **13** : 803.

11. FRANK, A. B. Sclerotienkrankheit der Kartoffel. *Loc. cit.* 500.

Kirchner (**7**) found potato plants which showed symptoms very similar to those in the lettuce, the stem rotting off just above the ground. Where the plants stood close together a vigorous growth of *Botrytis cinerea* appeared upon the affected parts, to which the author attributes the disease. No sclerotia were found. Ritzema Bos (**8**) found the same disease abundant in Holland. Cohn (**6**) notes a potato disease in Germany with very similar symptoms, but found sclerotia which seemed to belong to *Sclerotinia Libertiana*. The same is stated as being abundant in Norway. A "new disease of the potato" has been described by Smith (**1**), Wilson (**3**), and Blytt (**4**). The diseased plants became covered with a thick, felt-like growth of fungous mycelium, and in a short time stem and leaves were completely destroyed. Immersed in the mass of mycelium

appeared numerous black sclerotia, ranging in size from that of a grain of sand up to a small bean. From such sclerotia a Peziza form was obtained, which is shown, copied from Smith's figure, in *fig. 37*. The form was described by Berkeley and Wilson (3b) as a new species, under the name *Peziza postuma*. De Bary (5), however, to whom the material was sent, determined the fungus as *Sclerotinia Libertiana*. *Peziza postuma* is also given by Rehm (10, p. 816) as a synonym of *S. Libertiana*. In each of these cases the disease appears to have been caused by Botrytis or Sclerotinia alone, and no reason appears for claiming a connection between them.

CUCUMBER DISEASE.

BIBLIOGRAPHY.

1. HUMPHREY, J. E. Diseases of the cucumber plant. A sclerotium disease. Rept. Mass. Exp. Sta. 10: 212. 1893.

2. COOKE, M. C. Cucumber diseases. Gard. Chron. III. 14: 137. 1893.

The disease described by Humphrey (1) under the name of "timber rot" is not uncommon in cucumber houses in Massachusetts. The writer has met with it several times and also has received specimens from the New York Exp. Sta. at Geneva. Cooke (2) notes the occurrence of apparently the same trouble in England. The disease is characterized by a dry rot of the stem with a production of mycelium and sclerotia upon the surface. From the sclerotia *Sclerotinia Libertiana* readily develops. The writer has found no conidial form in connection with the disease. Humphrey, however, finding Botrytis on a decaying fruit, argues a connection between the forms. He obtained sclerotia in cultures from conidia which are stated to have shown complete identity in microscopic structure with sclerotia developed from the ascospores of the Sclerotinia. The form and manner of growth of the sclerotia were not the same, but this difference was ascribed to the nature of the substratum.

Humphrey's results have been repeatedly duplicated by the writer. It is true that Botrytis is often found on rotten cucumbers, and also that in cultures from conidia sclerotia may be

obtained indistinguishable in microscopic structure from those of *Sclerotinia Libertiana*. This has already been shown in connection with the lettuce disease. It was also shown there, however, that the form and manner of production of the sclerotia is highly characteristic and not affected by the substratum. There is, in short, no reason whatever for supposing, from this case, any connection between Botrytis and Sclerotinia except their occurrence in the same house. The entire distinctiveness of the two forms is nowhere more easily demonstrated than in such a case as this.

VEGETABLE, BULB, AND FRUIT ROTS.

BIBLIOGRAPHY.

1. COEMANS, M. E. Recherches sur la genèse et les métamorphoses de la *Peziza Sclerotiorum* Lib. Bull. de l'acad. roy. des sciences de Belgique II. **9**:62. 1860.
2. BREFELD, O. Untersuchungen die Fäulniss der Früchte betreffend. (Bot. Zeit. **34**: 28. 1876.)
3. WAKKER, J. H. (*a*) Vorläufige Mittheilungen über Hyacinthenkrankheiten. Bot. Centralb. **14**: 315. 1883.
   (*b*) Ueber die Infection der Nährpflanzen durch parasitische Peziza (Sclerotinia) Arten. Bot. Centralb. **29**: 309. 1887.
4. DE BARY, A. *loc. cit.*
5. KISSLING, E. Zur Biologie der *Botrytis cinerea*. Hedw. **28**: 227. 1889.
6. HALSTED, B. D. Fungous diseases of various crops. Rept. N. J. Agrl. Coll. Exp. Sta. **3**: 350. 1891.
7. MASSEE, G. (*a*) An onion disease. Gard. Chron. III. **16**: 160. 1894.
   (*b*) Onion Sclerotinia. Text-book of plant diseases 156.
8. POTTER, M. C. Rottenness of turnips and swedes in store. Journ. Board of Agr. **3**: 120. 1896.)
9. WEHMER, C. Untersuchungen über die Fäulniss der Früchte. (Zeitschr. f. Pflanzenkrankh. **6**: 173. 1896.)
10. OUDEMANS. Ned. Kruidk. Arch. II. **4**: 260.
11. SORAUER, P. Pflanzenkrankheiten.
12. FRANK, A. B. Die Pilzparasitären. Krankheiten der Pflanzen.

One of the most common cases of trouble caused by Botrytis and Sclerotinia is the rotting of various fruits, vegetables, etc. The writer has investigated a case of rotting of turnips found in Munich, Germany. Affected roots were not foul or badly decayed except in the worst affected portions, but showed

simply a slight discoloration and moist appearance of the flesh, no outward change appearing. No fungus was visible at first to the naked eye. When cut in two and kept moist over night a vigorous growth of *Botrytis cinerea* appeared on the affected parts, most abundant where worst affected and shading off toward the most recently affected portion, where no conidia developed. The interior was found to be filled with a vigorous mycelium similar to that in the lettuce and other diseases (*fig. 49*). Cultures on various media gave the usual Botrytis development, conidia being developed abundantly when badly affected tissue was used for infection, but very sparsely on newly affected portions or in cultures made therefrom. In the latter cultures sclerotia were quite numerous, being long, narrow, and thin, closely joined to the substratum in the characteristic Botrytis manner. It was found possible to infect sound roots with conidia by cutting out a plug, inserting the spores, and replacing the part cut out. There was no question that the rotting in this case was caused by *Botrytis cinerea*, pure and simple. The case described by Potter (8) is entirely similar. De Bary (4) and Coemans (1) found rotting of turnips, carrots, etc., caused by *Sclerotinia Libertiana* (*Peziza Sclerotiorum*). The writer has found by infecting turnips with Botrytis and Sclerotinia that an entirely similar effect is obtained and an intercellular mycelium produced which is quite indistinguishable. By making cultures, however, from the affected tissue, sclerotia are obtained, and in the one case conidia, which distinguish the two forms at once. This case, therefore, shows once more how easily confused these two forms are, having so similar a mycelium and effect, while at the same time it furnishes strong proof, when thoroughly looked into, of their entire distinctness.

Rotting of various fruits caused by Botrytis has been described by Brefeld (2) and Wehmer (9).

A rotting of onions is often caused by Botrytis and has been described by Halsted (6), Sorauer (11, p. 294), and Frank (12, p. 503). The writer found a similar case in Munich, where the affected tissue was permeated with a mycelium (*fig. 48*).

The Botrytis in this case was not a typical *cinerea*, having a low, dense manner of growth which persisted in cultures for many generations. The conidiophores were also short and stout (*figs. 5, 6*), and the conidia small and rather pointed as in **12**, plate 1. No sclerotia were found. Massee (**7**) ascribes the onion rot to *Sclerotinia bulborum* Wak. and figures (**7a**) a Botrytis apparently identical with *B. cinerea*, and a Peziza form showing no apparent distinction from *Sclerotinia Libertiana*. *Sclerotinia* (*Peziza*) *bulborum* was described by Wakker (**3**) as the cause of a hyacinth disease, a very interesting case in connection with the lettuce disease on account of its very similar mode of spreading and existence in the soil. No Botrytis stage was found, and Oudemans (**10**) states that none occurs. *Fig. 38* is copied from the latter. From all appearances it is doubtful whether the form described by Massee is the same as that of Wakker, and certainly the connection of the Botrytis and Sclerotinia forms, and their distinctness from the ordinary species, need further demonstration. An endless amount of confusion of these forms already exists on account of the multiplication of species for every new host.

III. Diseases caused by Botrytis alone.

No fungus is more common on dead or dying plant tissue than the common form of Botrytis. Not only is it abundant as a saprophyte, but cases often occur where it is a true parasite. Accounts of such cases are innumerable in botanical literature, but only a few can be briefly cited here. The species of Botrytis concerned has many different names, as has already appeared. In general it may be said that in Europe the ordinary form is referred to *B. cinerea* Pers., while in America the equally abundant species is usually called *B. vulgaris* Fr. These forms have been often regarded as identical, and the writer is able to state definitely that such is the case. Material from various parts of America and Europe has been carefully compared, both by examination and in cultures, from which it has been clearly shown that the forms are completely identical. On the basis of priority *cinerea* should be the specific name adopted, though, as

Wehmer[4] points out, *vulgaris* is more appropriate for so universal a species.

The following disease is a good type of this class:

A NEW DISEASE OF THE LINDEN.

In the spring of 1898, while working in Professor R. Hartig's laboratory at the University of Munich, the writer received several specimens of *Tilia parvifolia* which had been found in the nursery by Dr. von Tubeuf and appeared to be diseased. They were found among a considerable number of small saplings three to five feet high, growing close together in the usual nursery beds. At this time most of the trees were entirely leaved out, but these individuals had been noticed on account of their buds being not yet unfolded, though still green and apparently sound. The branches and upper part of the stem were also green and fresh, showing no abnormal symptoms, and the same was true of the roots. But in the lower part of the stem, from the surface of the ground up to a height of several inches, an abnormal condition was evident. Upon the surface of this part of the stem numerous excrescences were found, breaking out through the epidermis, with a thickness of about 0.5^{mm}, and varying greatly in shape and size. Some were nearly round, others irregular, and still others long and narrow, extending parallel with the stem, or more often around it. The latter form had a maximum length of about 2^{cm}, while the more circular ones had a diameter of 0.5^{cm}, or less. They had a dusty gray color and gave the stem an appearance somewhat like that of one affected with a Peridermium. *Text fig. 3* is from an excellent photograph of an affected stem, made by Dr. von Tubeuf. It was evident that the production of these excrescenses was proceeding from below upward, as the longest were just above the surface of the earth, while further up on the stem very small ones were just breaking out through the epidermis. In the affected part of the stem the wood and bark were discolored and evidently dead, but above and below it the tissue

[4] Zeitschr. f. Pflanzenkrankh. 4: 209. 1894.

was still fresh and sound. The bark appeared to be first affected, as it was always discolored somewhat in advance of the wood. Upon examining the outward excrescences it was found that the dusty appearance of the surface was due to a dense growth of a form of Botrytis, much like *cinerea*, but not entirely agreeing with the typical form. The conidiophores were very stout and thick, averaging 20μ in diameter, and the conidia large and very various in shape, many being nearly 30μ in length (*fig. 10*). In cultures the form at once reverted to the typical *cinerea*, showing that it belonged to that species. Further examination showed that these excrescences were a sort of half-formed sclerotia, having the usual cellular structure at the base, but lacking a definite surface layer and resolving above into a dense mass of conidiophores. *Fig. 40* shows a section of one of these sclerotia. They originate in the cortical parenchyma, being separated by the bast layer from the wood. Besides these sclerotia the cortical parenchyma was found to be permeated by a vigorous mycelium about as in the other diseases described. The affected tissue was being rapidly destroyed, but the bast layer seemed to be little affected and no filaments could be found in the wood except a few in the most outer portion.

FIG. 3.—Linden stem attacked by Botrytis.

The affected portion of a stem was split in two and the two halves placed in a moist chamber. In one night a luxuriant Botrytis growth developed, being confined entirely to the cortex, most abundant in the worst affected portion and shading off gradually in the direction of what had been the upper part of the stem. Toward the boundary between the affected and unaffected areas no Botrytis appeared, but an abundant mycelium. In this portion, *i. e.*, the most newly affected, there appeared later ordinary black sclerotia having a long narrow form and located in the cortex, especially along the cut edges. The Botrytis gradually advanced, but was much more abundant back in the older part. Gelatine cultures were made with conidia and portions of the affected bark. The former produced a considerable mycelium, rather few conidia, and some sclerotia. The latter developed a similar mycelium,very few conidia, and numerous, larger, roundish sclerotia. Cultures were also made in the portions of the vegetative mycelium which appeared in the moist chamber upon the most newly affected portion of the stem (where no Botrytis appeared). This gave a vigorous mycelium with sclerotia, but no Botrytis. All of the sclerotia obtained from this material showed the characteristics of those of the botrytis type of the lettuce disease, being thin and joined with the substratum.

Several more affected trees were found in the nursery, both *Tilia parvifolia* and *T. grandifolia*. These showed the same symptoms as before. Some that were most affected seemed to be quite dead, and in the lower part of the stem the bark was quite destroyed, the wood being laid bare, but covered more or less with shreds of the bast which still remained. A few ordinary black sclerotia were found, but most were of the half-formed variety, covered with Botrytis. These appeared to have developed the previous fall, producing conidia in the spring.

The main features of this disease are these: a vigorous mycelium, starting apparently at the surface of the ground, proceeded upward through the cortical parenchyma, completely destroying it and eventually killing the plant. Sclerotia were developed upon the surface but reverted to the production of

conidia of *Botrytis cinerea* before becoming mature. This may have been due to the coming on of winter before the sclerotia were fully formed; at any rate the fungus was able to develop sclerotia and conidia in the usual manner, as shown in cultures and the moist chamber. It is believed that this disease was caused solely and primarily by *Botrytis cinerea*, in this case a true parasite. Cultures and observations showed throughout the same characteristics as found in Botrytis in connection with the lettuce disease and there is no reason to suppose that any other species was involved. This interesting disease upon the linden appears to be an entirely new one, and is the first of this class to be reported upon a woody plant. Its similarity, however, to some of the other stem rots herein described is apparent.

BOTRYTIS ON ROSE TWIGS.

Some twigs of hothouse roses were obtained in Munich by the writer, which were affected by a dying away of the tips, the disease gradually extending down the stem. The extreme tips were entirely dead and covered with a Botrytis growth. Further down the stems were turning black and dying, but no Botrytis was visible. Sections showed that the interior of affected parts of the stem was full of filaments. In the worst affected parts the whole tissue was destroyed and Botrytis conidiophores were growing out through the surface. In the less affected parts it was found that the disease advanced by large filaments which grew at first through the area of bast fibers, entirely disorganizing this tissue before the rest was at all affected. Later the whole stem became included. *Figs. 46* and *47* show cross and horizontal sections of affected twigs with the filaments among the bast fibers. It appeared in this case, as in several others already described, that the most actively parasitic filaments which attack new tissue bear no conidia, the latter appearing later on the older parts. The species was the usual *cinerea* but was especially luxuriant, bearing large, many-branched conidiophores. No sclerotia were found upon the limited material at

hand, but cultures from the Botrytis gave at first conidia and later sclerotia of the usual botrytis type.

Among the many other diseases of this class which have been described, space only permits that the following be mentioned:

CONIFERS.

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RITZEMA BOS, J. Forstlich-naturwiss. Zeitschr. 6:174. 1897.
MASSEE, G. Text-book of plant diseases 160.

GRAPE.

MÜLLER-THURGAU, H. Landwirtsch. Jahrb. 17:83. 1888.
VIALA, P. Rev. gén. de bot. 3:145. 1891. (Zeitschr. f. Pflanzenkrankh. 7:159. 1897.)
RAVAZ, L. Compt. rend. 118:1289. 1894. (Zeitschr. f. Pflanzenkrankh. 5:49. 1895.)
CUBONI, G. Bull. di Notizie Agrarie. 2:487. 1896. (Zeitsch. f. Pflanzenkrankh. 7:159. 1897.)
VON BABO UND MACH. Weinbau.

LILY.

WARD, H. M. Ann. Bot. 2:319. 1888. Diseases of plants 117.
KEAN, A. J. Bot. Gaz. 15:8. 1890.
MASSEE, G. Text-book of plant diseases. 161.

HORSE CHESTNUT.

KISSLING, E. *Loc. cit.*

PRUNUS TRILOBA.

TUBEUF, K. F. VON. Pflanzenkrankheiten 281.

GENTIAN.

KISSLING, E. *Loc. cit.*
PRILLIEUX ET DELACROIX. Bull. Soc. Myc. de France 6:135. 1890.

CYCLAMEN AND PRIMULA.

WEHMER, C. *Loc. cit.*

In all these cases the general nature of the disease was the same, Botrytis appearing more or less on affected parts and often forming sclerotia. Many interesting points are brought out in some of the descriptions, but they have little bearing on the question under consideration. It may be mentioned that the

Botrytis Douglasii of Tubeuf is without any doubt a form of *B. cinerea*, as the writer has ascertained by examination of the original material in cooperation with Dr. von Tubeuf. In Professor Ward's lily disease the species was thought to be distinct from *cinerea* on account of the large size of the conidia (20–25 × 15μ). The writer has often found the ordinary species with spores as large as 30–15μ, however, and it would seem from Professor Ward's figures of the conidiophores that the form must be very close to *cinerea*. In some of these cases, notably that of the grape, the Botrytis is referred to *Sclerotinia Fuckeliana* De By., its supposed Peziza form, which is said to develop from sclerotia on affected grapes. This form is unknown to the writer, but has been held by De Bary to be the real mature form of *Botrytis cinerea*. Pirotta (N. Giorn. Bot. Ital. **13**: 130. 1881) has also described *Fuckeliana* as distinct from *Libertiana*, but it is apparent in almost all cases where *B. cinerea* is referred to as *Scl. Fuckeliana* that nothing more was observed than the ordinary conidial form and possibly sclerotia. Whether or not this is the true perfect form of *cinerea*, it is certain that the connection has never been proved directly, and much has been taken for granted by various writers upon no foundation whatever.

IV. Diseases caused by Sclerotinia Libertiana alone.

Cases are not rare of *Sclerotinia Libertiana* attacking plants when no Botrytis appeared. The cucumber disease already described is really one of this sort, as the Botrytis simply happened to occur in the same house. The writer has seen water cress and parsley in greenhouses attacked by this species, such cases being not uncommon in the Boston houses where these plants are considerably grown. Tomatoes also occasionally show the same trouble, rotting at the surface of the ground. The Peziza form is occasionally found developing from sclerotia in the soil in such houses.

De Bary (*loc. cit.*) describes a stem rot of Zinnia, Petunia, and other plants caused by this species. It is also not uncommon upon Helianthus. Dr. O. Kirchner, of Hohenheim, gave

the writer Peziza-bearing sclerotia from such a disease of this plant. Pammel (Trans. St. Louis Acad. **6**: 191. 1893) has described a similar disease. W. G. Smith (Gard. Chron. III. **8**: 324. 1890 and III. **9**: 791 1891) describes a stem rot of hollyhocks caused by *Scl. Libertiana*. The disease was entirely similar in all these cases and needs no extended description. The stem of affected plants rotted just above the ground, being filled with a vigorous mycelium as in the diseases already described. Sclerotia were produced both upon the surface and in the interior cavity of the stem, from which the Peziza form readily developed.

A disease of clover has been described by several writers which is very similar to those under consideration but ascribed to *Sclerotinia Trifoliorum* Erik. which is regarded as distinct from *Libertiana* though apparently very similar. The writer received alfalfa plants from Mr. F. C. Stewart of the New York Exp. Station which were supposed to be affected with this species. The sclerotia, however (*text fig.* 1 *e*), both from diseased stems and cultures, were entirely similar to those of *Libertiana*, and produced a Peziza form which left no doubt that it was that species.

V. General conclusions on Sclerotinia Libertiana and Botrytis cinerea.

During the four years in which this work has been carried on a great deal has been done which has no special connection with that part of the subject with which the present article deals. A large amount of material has been obtained and the fungi grown and studied under all sorts of conditions. Most of the results which it is intended to emphasize here have already been brought out in various places in this description. It is maintained above all *that Sclerotinia Libertiana and Botrytis cinerea have no connection whatsoever with each other, and that the former species has no conidial stage of this type.* Growing either as a saprophyte or parasite, it shows at all times a mycelium composed of large, branching, septate filaments, averaging about 10–15 μ in diameter, which produce

organs of attachment abundantly when in contact with any hard substance. Sclerotia are always produced abundantly in cultures and upon affected plants. These vary in size up to an inch in length, having an irregular form, but are solid and "meaty" and produced embedded in the mycelium, having no connection whatever with the substratum. The Peziza form is readily obtained from them. The internal structure of these sclerotia consists of a mass of thickened filaments knotted closely together and surrounded by a black, cellular layer. This species is a typical example of a facultative parasite, being able to exist indefinitely as a saprophyte but at the same time capable of attacking a great variety of plants in a strictly parasitic manner.

Botrytis cinerea is without doubt a closely related species, and has many points of resemblance. It is not as strongly parasitic as the other species, attacking living plants more commonly only when they are under unfavorable conditions or when injured in some way. At times, however, it appears to be a true parasite. When growing as a saprophyte it has no particular resemblance to *Scl. Libertiana* under the same conditions, producing much less mycelium and a great abundance of conidia. When growing as a parasite it is in some respects indistinguishable from the other species. The mycelium is entirely similar and organs of attachment are produced which are likewise exactly the same. The effect upon the plant is often entirely similar. As a parasite it appears to produce fewer conidia in proportion to the degree of parasitism. Often in newly affected tissue none appear. Sclerotia are often produced in cultures and on affected plants but with considerable uncertainty. Not rarely cultures made from conidia produce no spores whatever, but numerous sclerotia. This is most common when parasitic material is used. The sclerotia are highly characteristic and suffice at all times to distinguish this species from the other. They usually have a narrow form, especially in tube cultures, and are always thin and inseparably attached to the substratum, lacking entirely the definite form and the solid, "meaty" structure of the sclerotia of *Scl. Libertiana*. So far as known no Peziza has ever

been obtained from sclerotia developed from *Botrytis*. On the basis of internal structure these sclerotia cannot be clearly distinguished from the others. They vary in compactness and seem to have no very characteristic makeup. The two species often occur together, as Botrytis does in connection with many other fungi, and it is believed that the only unprejudiced argument which has ever existed in favor of the connection between *Sclerotinia Libertiana* and *Botrytis cinerea* is their frequent simultaneous occurrence, in connection with the similarity of the mycelium and the fact that they often attack plants in a very similar manner; all of which is explained by their close relationship. When carried further than this they may be readily separated and distinguished from one another and the distinctive characters brought out which have been described.

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Amherst, Mass.

EXPLANATION OF PLATES XXV–XXVII.

PLATE XXV.

FIG. 1. Typical conidiophore of *Botrytis cinerea* Pers.

FIG. 2. Portion of same, more enlarged.

FIG. 3. Conidiophore from old, exhausted culture.

FIG. 4. Botrytis slightly enlarged.

FIGS. 5–9. Botrytis from onion.

FIGS. 10–11. Conidia of *Botrytis cinerea*.

FIG. 12. Conidia of Botrytis from onion.

FIGS. 13–17. Development of conidiophore of *Botrytis cinerea* from mycelium within a plant.

FIG. 18. Development of terminal branches.

FIGS. 19–22. Forms of organs of attachment.

PLATE XXVI.

FIGS. 23–25. Forms of organs of attachment.

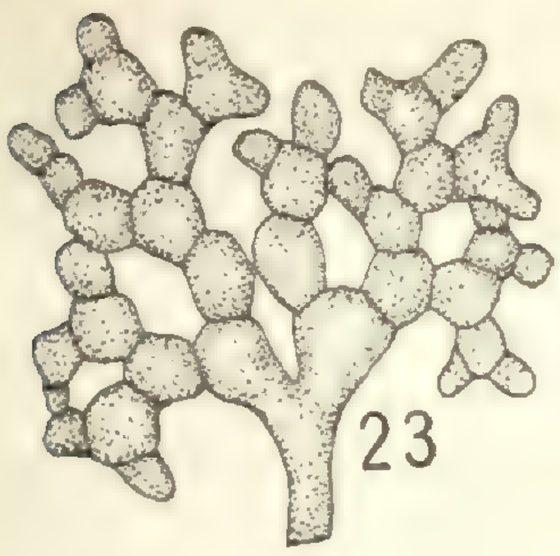
FIG. 26. Tip of a branch of an organ of attachment growing against glass.

FIG. 27. Mycelium of Botrytis from stem of lettuce seedling, causing "damping off."

FIG. 28. Cross connections in Botrytis mycelium.

FIG. 29. Filaments of *Sclerotinia Libertiana* Fckl., entering lettuce leaf.

SMITH on BOTRYTIS AND SCLEROTINIA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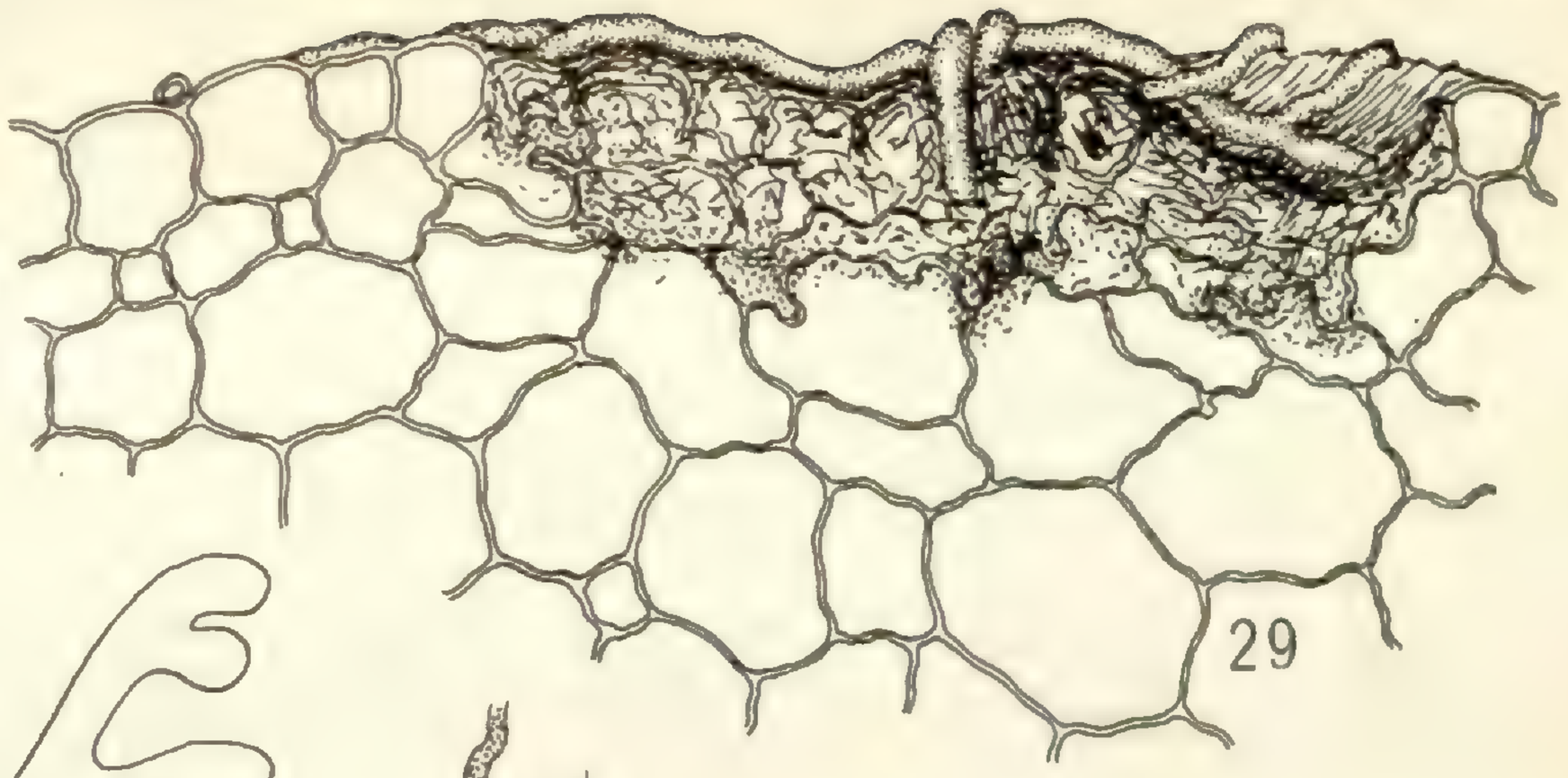
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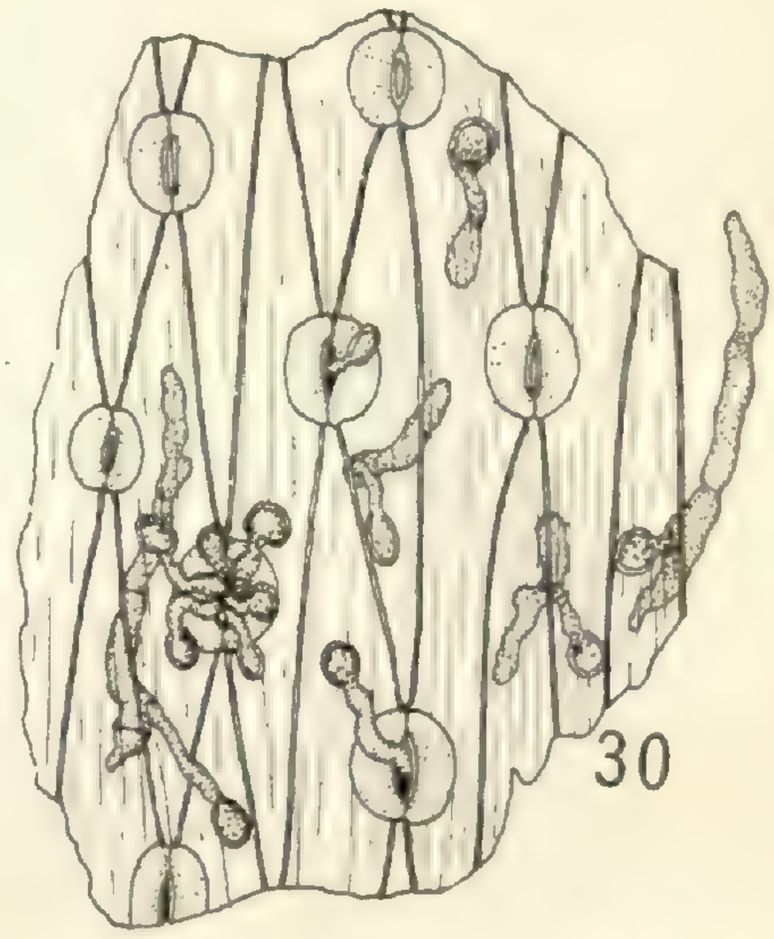
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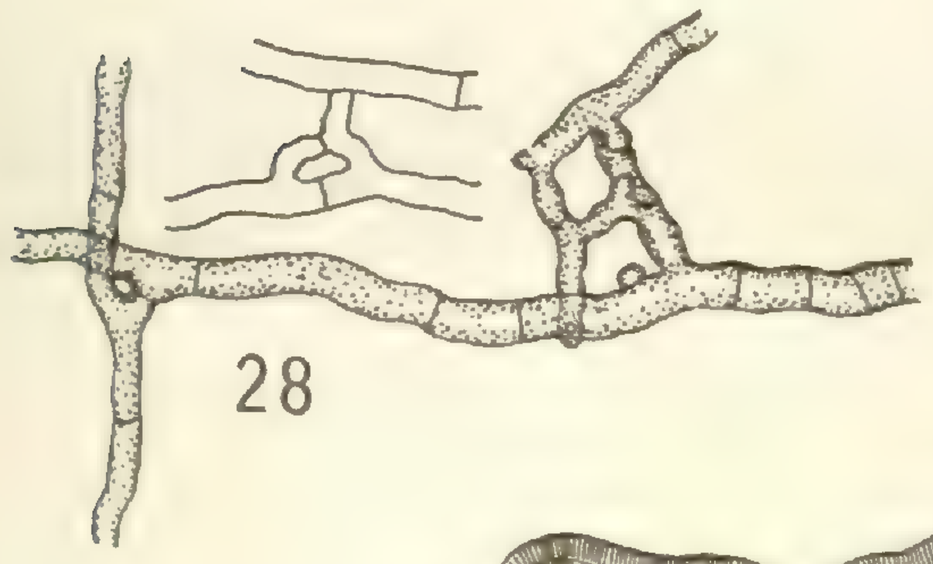
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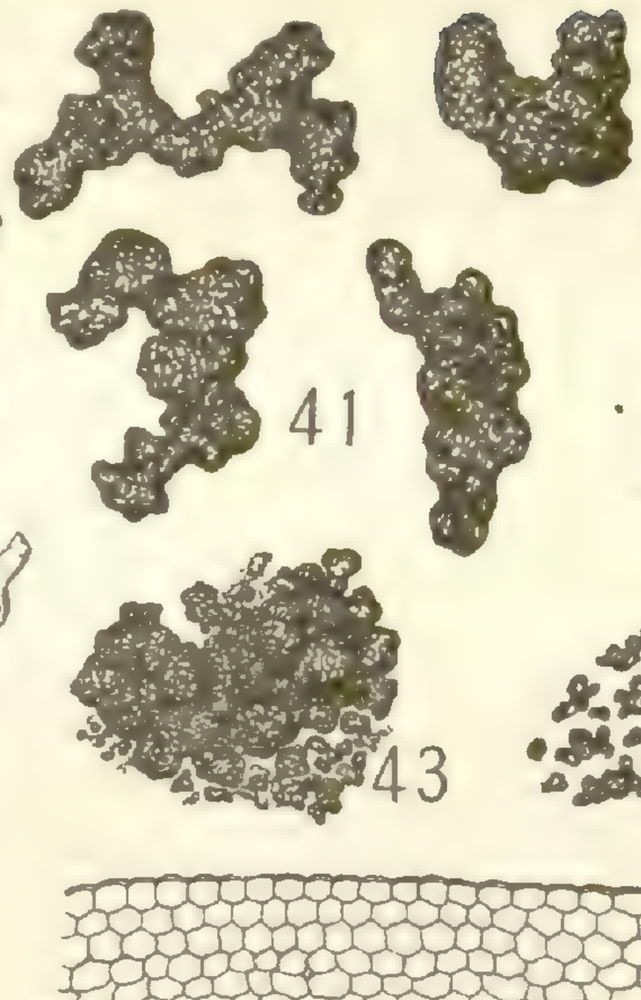
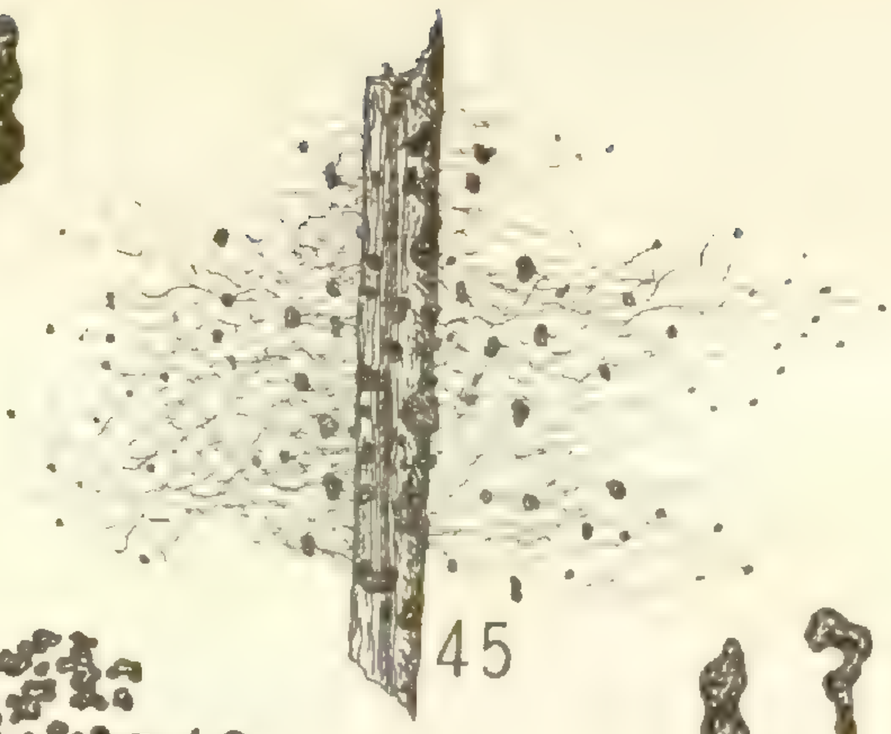
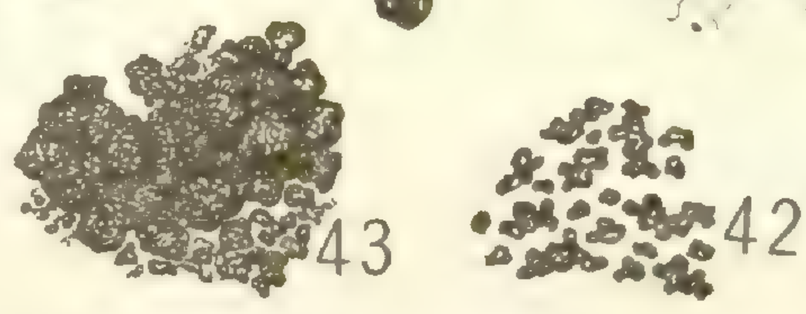
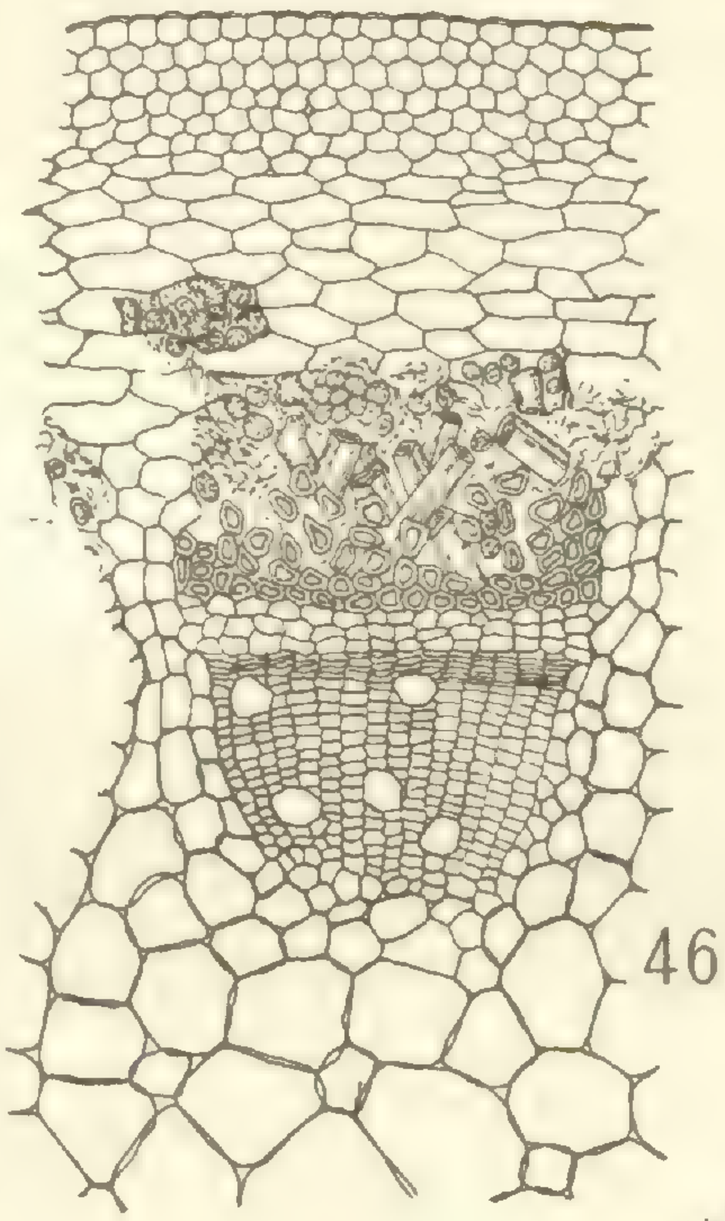
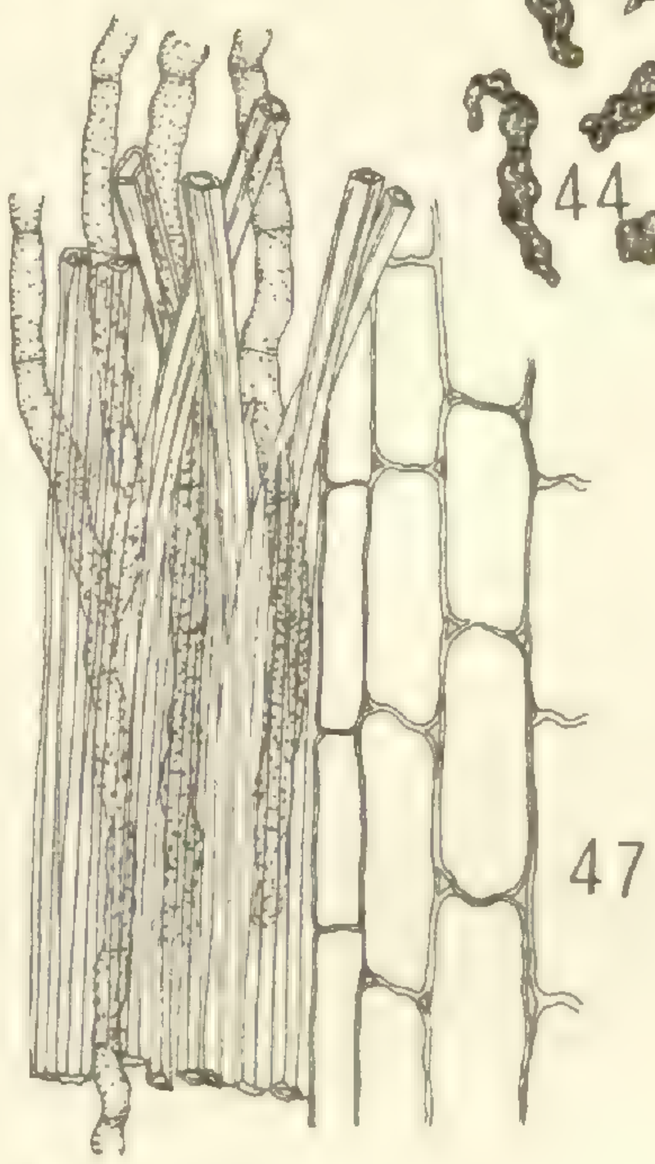
SMITH on BOTRYTIS AND SCLEROTINIA











Figs. 40–51

SMITH on BOTRYTIS AND SCLEROTINIA

FIG. 30. Conidia of *Botrytis cinerea* germinating on and entering epidermis of an onion leaf.

FIG. 31. Mycelium of *Scl. Libertiana*, with organs of attachment on surface of lettuce leaf.

FIG. 32. Longitudinal section of Peziza fructification of *Scl. Libertiana*.

FIG. 33. Asci and paraphyses of same, more enlarged.

FIG. 34. Commencement of formation of a sclerotium.

FIG. 35. Peziza stalk arising from a sclerotium.

FIG. 36. Mature Peziza form.

FIG. 37. *Peziza postuma* B. & W. (Copied from Smith.)

FIG. 38. *Sclerotinia* (*Peziza*) *bulborum* Wak. (Copied from Oudemans.)

FIG. 39. Cross section of sclerotium.

PLATE XXVII.

FIG. 40. Section of Botrytis sclerotium from linden.

FIG. 41. Typical sclerotia of *Sclerotinia Libertiana*.

FIG. 42. Small sclerotia from lettuce.

FIG. 43. Sclerotial crust formed by lettuce fungus.

FIG. 44. Sclerotia of *Botrytis cinerea*.

FIG. 45. Formation of secondary sclerotia.

FIG. 46. Cross section of rose twig, showing Botrytis filaments in the bast.

FIG. 47. Longitudinal section of same.

FIG. 48. Botrytis filaments in onion.

FIG. 49. Botrytis (or Sclerotinia) filaments in turnip.

FIG. 50. Sclerotinia (or Botrytis) filaments in lettuce leaf, advancing into sound tissue.

FIG. 51. Sclerotinia (or Botrytis) filaments in badly affected lettuce stem.

A CONTRIBUTION TO THE LIFE HISTORY OF QUERCUS.

CONTRIBUTION FROM THE HULL BOTANICAL LABORATORY. XIX.

ABRAM H. CONRAD.

(WITH PLATES XXVIII AND XXIX)

THE material for this study was all collected in the vicinity of the University of Chicago in the spring and summer of 1898. Gatherings of several species were incidentally made, but *Quercus velutina* Lam. (*Q. coccinea tinctoria* Gray) afforded the most complete series, and as my investigations have been devoted chiefly to this species, it is alone considered in this paper.

In dealing with material so refractory as Quercus one seldom secures a satisfactory series during a single season of collecting. The difficulties to which I here refer are due in part to the stubbornness with which the material resists the penetration of fixing agents, and in part to the remarkable uniformity with which any stage occurs in all the ovules at the same time. This bars one from an opportunity of retrieving any loss from the mismanagement of a batch of material. Detailed cytological observation has not been attempted, the object having been rather to determine the nature, order, and time of events as they occur in the gametophyte generation.

Except the brief account of Quercus by Miss Benson in her work on the Amentaceæ, I have no knowledge of any attempt to work out the life history of the genus.

The work was done under the guidance and encouragement of Dr. John M. Coulter and Dr. Charles J. Chamberlain, to whom my thanks are due.

MATERIAL AND TECHNIQUE.

During late winter and early spring collections were made at intervals of several days, with a view to determine the stage of

development in which the several structures pass the winter, and the sequence of their development as it occurs in the spring. Beginning with May 5 and continuing to July 7, gatherings were made at intervals of two or three days, and in order that the material might be typical it was mostly taken from the upper branches of a single thrifty tree.

Owing to the protective covering of scales and glandular hairs which prevented the penetration of fixing and imbedding agents, great care was exercised in removing this so as to expose freely the structures to be investigated. Several fixing agents were tried, but chromo-acetic and picro-acetic were most satisfactory. The chromic agent preserved the material well, but rendered it more brittle and difficult to section. The picric agent is to be preferred. The chromo-acetic was a 1 per cent. aqueous solution of chromic acid with $\frac{1}{2}$ per cent. acetic acid. The picro-acetic was a saturated solution of picric acid in 70 per cent. alcohol with 0.5 per cent. acetic acid. The chromic fluid proved best when the material was wet in 95 per cent. alcohol, and quickly passed into the fixing agent. The picric was most satisfactory when used at a temperature of 80 to 90 degrees Centigrade.

Thus fixed, the material was dehydrated with successive grades of alcohol, passed into xylol, imbedded in paraffin, cut in serial sections 5 and 10 μ in thickness, and stained upon the slide. Several stains were tried. Cyanin and erythrosin proved good for early stages, Delafield's haematoxylin for archesporial stage, and fuchsin and iodine green for embryo-sac and embryo.

THE STAMENS AND POLLEN.

Material collected in early spring (March 7) may be taken as fairly representing the stage of development in which the microsporophylls pass the winter. While the structure is well differentiated into filament and anther, the latter consists of a mass of apparently uniform cells (*figs.* 1, 2). Upon the approach of a growing temperature there occurs a rapid development and a corresponding early differentiation into the usual regions of

sporogenous, tapetal, and wall tissues, the latter comprising two to four layers of cells (*fig. 3*). These groups of cells exhibit nothing unusual either in their development or destiny. The inner wall cells are the first to break down, contributing their substance to the cells within and leaving the tapetum to form a sheath which incloses and nourishes the sporogenous cells. Before the final disintegration the cells of the tapetum show numerous prominent nucleoli, and quite generally become binucleate. The two nuclei are plano-convex or concavo-convex, with their plane or concave surfaces facing each other (*fig. 6*).

The spore mother-cells increase in size, separate, and form the usual tetrads (*fig. 4*). The mature spore has a smooth surface, is somewhat angular, and has a diameter of about 30 μ. The exospore has three points of weakness, which seem to correspond to the three exterior angles of the tetrad, and which afford points of easy rupture to the tube in germination. At the time the spores are discharged, a small proportion of them show that the division into the tube and generative nuclei has occurred, the latter being the smaller and lenticular in form. Each contains a single prominent nucleolus (*fig. 5*). The subsequent history of the microspore was not satisfactorily traced. The difficulties of following it through the interval of thirteen months intervening between pollination and fertilization are multiplied by a copious development of nucleated hairs which takes place in the loculus during the interval. Three attempts were made at artificial germination of the pollen but without success. In 1898 the pollen of *Q. velutina* was shed May 17 and 18 in the vicinity of Chicago.

THE OVULE.

The first indication of an ovule is manifest after the renewal of growth following a period of about eleven months of arrested ovarian development. *Fig. 7* represents a transverse section of the ovary on the date of March 7, and shows the condition attained during the first year of growth. The three carpels are so fused as to form three nearly distinct loculi. These communicate with one another at the base, but in the middle and

upper regions they are separated by the complete fusion of the carpels. Each loculus contains two prominent placental folds (*fig.* 7, *hh*), and numerous hairs developing from the inner surface of the carpel. *Fig.* 9 is a longitudinal section through a carpel from material collected April 21. *Fig.* 10 is a transverse section through the placental folds, which mark what may be regarded as the beginning of ovular development.

Material collected May 5 shows the first indication of the integuments (*fig.* 11, *ee*). The nucellus now rapidly elongates by active cell growth and division, especially in the basal region. The integuments push forward at a still more rapid pace, and in a short time completely inclose the nucellus. In the meantime, growth being more active in the outer angle of the base of the ovule, it is forced to an erect position.

ARCHESPORIUM.

About the time the nucellus is fairly inclosed by the integuments there is a mass of from twenty to sixty or more cells in its upper half which clearly manifests an archesporial character. This character is manifested by a larger and clearer nucleus, a coarser linin net work, and larger granules, in contrast with the nuclei of the surrounding cells, while the cytoplasm takes a much deeper stain with Delafield's heamatoxylin. In *figs.* 14–20 the extent and position of this archesporial mass is indicated. Many ovules showing this stage were sectioned and figures could be indefinitely multiplied.

In view of the usual record of events as they occur in the development of megaspore in angiosperms this archesporial mass is marked by two striking peculiarities: (1) its unusual abundance, and (2) the cells are potential megaspores as is proved by subsequent events. While multiple megaspores are known to occur in *Rosa livida*, and some of the Amentiferæ, Ranunculaceæ, Rubiceæ, and a few others, Casuarina is probably the only case hitherto known which strikingly resembles Quercus in this regard.

This archesporial stage is of relatively long duration, apparently a period devoted to the accumulation of energy to be

expended in the important changes which follow in rapid succession.

EMBRYO-SAC.

At length certain cells centrally located in this archesporial mass indicate by a thickening of the linin network, enlargement of the granules, and a coarser appearance of the nucleus, that they are entering the prophase of mitosis. The nucleoli of such cells contrast with those of neighboring cells in size and staining qualities.

Before the spirem is formed the race is usually yielded to a single vigorous cell, apparently the fourth or fifth below the surface. This cell, improving the advantage thus accorded, crowds upon its sister cells, and they in turn may soon show evidence of collapse. *Figs. 21* and *22* show a condition not uncommon, in which some of the adjacent cells are in advanced stage of deterioration, while in other instances the neighboring cells show little evidence of breaking down when the spirem is formed in the fertile megaspore (*figs. 24, 25*). It is not unusual to find the condition represented in *fig. 23*, in which the nuclei of cells in the apical region of the nucellus, previous to the spirem stage of the fertile megaspore, contain numerous small nucleoli, presumably the fragments of a single large nucleolus common to all healthy cells, and whose fragmentation may be regarded as an early evidence of the deterioration of the cell.

Inasmuch as these more marked cells usually bear a lineal relation to each other, it might suggest the usual type of tapetal cells, potential and fertile megaspores recorded for angiosperms. The events leading to this condition, and those that follow, preclude this hypothesis; and in addition it may be said that the axial position does not always obtain. Such cells may lie side by side, or they may be separated by one or more intervening cells.

As stated above, it is usual that but a single archesporial cell proceeds so far as to form the spirem. It is, however, not always the case. *Fig. 29* shows a well-defined exception. It shows two well-formed spindles with the chromosomes arranged

upon the equatorial plane. The number and form of the chromosomes are so markedly different from those of the vegetative cell that they afford conclusive evidence that the divisions are of the reduction type, and in view of all the circumstances it can scarcely be doubted that it is the first division in fertile megaspores. In *fig. 31* we have a case in which two adjacent megaspores have reached the four-celled stage. Considering the large number of archesporial cells, and the frequency with which a number of these undergo early mitotic phases, it has been a matter of surprise that the phenomenon of a two-celled stage or a four-celled stage in more than one megaspore in the same nucellus does not more frequently occur. This condition, however, we may better appreciate when we have learned more of the causes which determine the fate of a cell.

The first division observed in the apical region of any mature nucellus is shown in *figs. 26* and *27*. This is believed to be the spirem stage of the first division of the megaspore. The thread is small and I am unable to determine whether or not it conforms to the mode of splitting commonly ascribed to spore mother cells. Whatever weight, however, may be attached to synapsis as restricted to such division obtains here. Material collected June 4 and 5 afforded many cases of the fertile megaspore presenting phases illustrated in *figs. 21–27*. The transition to the four-celled stage of the embryo sac is accomplished with speed and marked uniformity of time in all the ovules. Material collected June 5 showed early phases up to and including the spirem stage of the first division of the megaspore to be quite common (*figs. 21–25*), while material collected two days later showed the four-celled stage of the sac with corresponding frequency.

Notwithstanding a large number of ovules in which the two-celled stage might be sought were sectioned, *fig. 28* probably illustrates the most satisfactory case of a two-nucleated sac. It shows two deeply stained masses which I take to be the two unorganized daughter nuclei of the first division of the megaspore, and in no case did I find two nuclei in the so-called resting stage.

In view of all the evidence, I cannot escape the conviction that the first division that occurs in the archesporium of the mature nucellus is quickly followed by a second division without the previous reorganization of the nuclei of the first division, and that this results in the four-nucleated embryo sac.

Not only does the space of two days seem sufficient for the transition from the one-celled to the four-celled stage, but in some instances development had exceeded this. It was in material collected June 7 that I found the most satisfactory illustration of the eight nuclei of the sac (*fig. 32*). Here the synergids and oosphere are in the micropylar region, the three antipodals in the base of the sac, and the polar nuclei in the act of fusing in the middle region. In this instance I find no evidence that the pollen tube has made its approach, yet in view of its elusive character it would be unsafe to affirm that it has not done so. Several cases of the fusion of the polar nuclei were observed, but the presence of the antipodals was usually a matter of doubt. This, however, is to be expected, when we consider the usual ephemeral nature of these cells, and since their nuclei possess no character which distinguishes them from the nuclei of the disintegrating cells of the nucellus, it is not an easy matter to identify them.

About the time the four-celled stage is reached, the embryo-sac begins to enlarge rapidly at the expense of the nucellar tissue, and by the time of the fusion of the polar nuclei, or soon after, the nucellus has almost entirely broken down. There is usually a fragment of the nucellus extending from the chalazal region a short distance up one side. This gives to the embryo-sac a somewhat pointed base, which is the only structure observed suggestive of the so-called *caecum*.

The synergids crowd well up into the micropyle, and display that striated beaked structure noted by observers in some other plants. *Fig. 34* in no way exaggerates the prominence of these striated tips, and, as Chamberlain observed in Salix, these tips may persist for a considerable time as a plug in the micropylar end of the sac.

The course of the pollen tube in relation to the synergids I have been unable to determine. In the most positive case of a pollen tube within the embryo-sac the course seems to have been between the synergids and the wall. Many cases were found of an open micropyle strewn with mucilaginous residue, indicating that the tube had passed, but a most careful search failed to reveal its presence within the sac. It is not unusual to find in the micropylar region of the sac numerous refractive starch granules, suggestive of the rupture of the tube and the discharge of the male cell, but the fusion with the nucleus of the oosphere was not observed.

ENDOSPERM.

There is a very early and copious development of endosperm. I have no proof that this begins before the fusion of the male cell with the oosphere, yet its universally prompt appearance when the sac reaches maturity seems to me to indicate a doubtful time relation. This early appearance of endosperm is a source of perplexity in the investigation of male cells and antipodals. The nuclei of the endosperm lie free in the stratum of protoplasm about the wall of the embryo-sac, and the cells show no evidence of running in walls up to the time at which the embryo cuts off cells to form the dermatogen. *Fig. 36* shows the condition of the endosperm as it occurs in connection with the embryo illustrated in *fig. 39*.

EMBRYO.

The embryo is anchored to the endosperm in the micropylar region by a short but distinct suspensor. The suspensor, at first a single cell, divides once by a vertical wall after the first few divisions have occurred in the embryo. *Fig. 37* shows the embryo of four cells while the suspensor is still undivided. At some time after this, and probably about the time the embryo cuts off cells to form the dermatogen, the vertical division occurs (*figs. 37–39*).

SUMMARY.

1. Winter buds show the stamens well formed, but with no perceptible differentiation of the cells of the anther. The carpels are also evident but relatively more rudimentary.

2. With the early growing conditions of spring there occurs the usual differentiation of the anther into sporogenous, tapetal, and wall cells. The sporogenous cells separate and form tetrads in the usual manner. The inner wall cells are the first to break down. The tapetal cells form a sheath about the spores, become binucleate, and break down shortly before the spore reaches maturity. A relatively small proportion of the spores show the division into generative and tube nuclei while still in the anther.

3. During the first year the carpels fuse so as to form three nearly distinct loculi each with two placental folds, upon each of which a single ovule develops, but the first indication of an ovule appears some time after the renewal of growth the following spring.

4. About the time the nucellus is inclosed by the integuments there is manifest in its upper half a mass of from twenty to sixty or more cells of distinct archesporial character. This character is evidenced by a larger and clearer nucleus with coarser linin network and larger granules, and by the cytoplasm of the cell taking a deeper stain than that of neighboring cells.

5. At length certain cells in the archesporial mass show a tendency to develop into megaspores. The race is usually yielded to a single cell which develops directly into the megaspore, the second division quickly following the first without the previous reorganization of the daughter nuclei of the first division.

6. Occasionally more than one cell in the same nucellus reaches the four-nucleate stage of the embryo-sac.

7. The mature embryo-sac contains the usual two groups of four nuclei each. There occurs an early fusion of the polar nuclei, followed by a copious development of endosperm which shows no tendency to run in walls up to the time when the embryo is well differentiated.

8. The first division of the oospore is transverse, and the suspensor undergoes but one subsequent division, which is vertical.

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EXPLANATION OF PLATES XXVIII–XXIX.

The figures are reduced from drawings traced by means of a Bausch and Lomb camera. Nos. 1, 9, 12, 13 were made with Reichert objective no. 7; the others with a Spencer or a Bausch and Lomb $\frac{1}{12}$ oil immersion with ocular combination magnifying 1200 and 1300 diameters.

FIG. 1. Longitudinal section through two stamens showing winter stage.

FIG. 2. Section of an anther, same date as above, showing cells of uniform character, more highly magnified.

FIG. 3. Section of anther of date April 22; shows differentiation into wall, tapetal, and sporogenous regions; the inner wall cells showing evidence of collapse.

FIG. 4. The formation of tetrads from the pollen mother cell.

FIG. 5. The mature spore with generative and tube nuclei.

FIG. 6. Two tapetal cells showing the binucleate and multinucleolate condition preceding final disintegration.

FIG. 7. Transverse section of the ovary showing loculi and placental folds (*hh*); March 7.

FIG. 8. A section of the placental fold more highly magnified; March 7.

FIG. 9. Longitudinal section of a carpel; marks the beginning of the ovule and the development of hairs from the inner surface of the carpel; April 21.

FIG. 10. Transverse section of the placental fold; April 21.

FIG. 11. Section of the ovule showing the first indication of the integuments (*ee*); May 5.

FIG. 12. Outline of the transverse section of the ovary showing the three loculi each containing two ovules; one loculus shows the hairs with which the cavity becomes almost completely filled; the ovules, nearly enclosed by the integuments, have assumed a position almost at right angles to the plane of the section.

FIG. 13. Outline of the section of the nucellus with its integuments; date same as *fig. 12*.

FIGS. 14–20. Longitudinal section of the nucellus showing the extent and position of the archesporial cells; dates ranging from May 13 to May 22; *fig. 20* is a section almost at right angles to the long axis of the nucellus.

FIG. 21. A row of five cells showing a tendency to develop into megaspores; the middle cell has taken the lead and the cells immediately above and below are breaking down.

FIGS. 22–25. Early prophases of mitosis in the first division of the megaspore.

FIGS. 26–27. Spirem stage of the first division of the megaspore.

FIG. 28. The unorganized daughter nuclei of the first division of the megaspore.

FIG. 29. Two megaspores in the same nucellus in act of first division, showing symmetrical spindles, with short and dense chromosomes arranged upon the equatorial plane, suggestive of reduction division.

FIG. 30. Four-celled stage of embryo sac; June 10.

FIG. 31. Two embryo-sacs in the same nucellus in the four-celled stage.

FIG. 32. Embryo-sac with the usual eight cells; shows the fusion of the polar nuclei in the middle portion of the sac.

FIG. 33. Embryo-sac with two synergids and oosphere in the micropylar region, and the polar nuclei in the act of fusion.

FIG. 34. Synergids with prominent striated beaks crowding into the micropyle.

FIG. 35. Synergids in the micropylar end of the sac and the oosphere suspended below.

FIG. 36. Endosperm showing the absence of any tendency to form walls at the time of embryo development represented in *figs. 38-39*.

FIG. 37. Four-celled embryo with one-celled suspensor.

FIGS. 38–39. Embryos showing periclinal division of dermatogen cells *fig. 39* more highly magnified.

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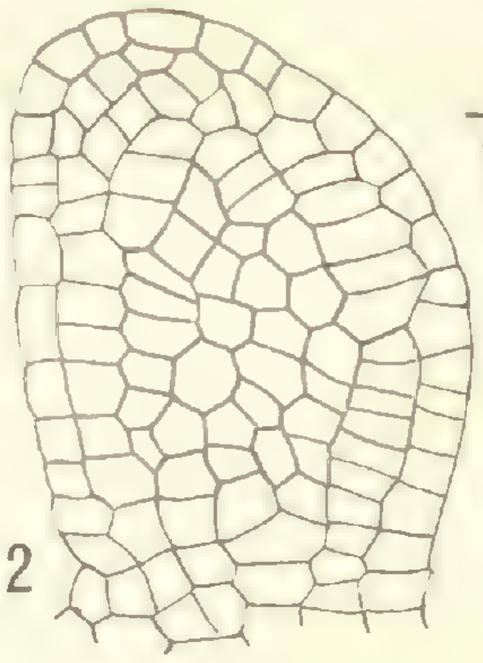
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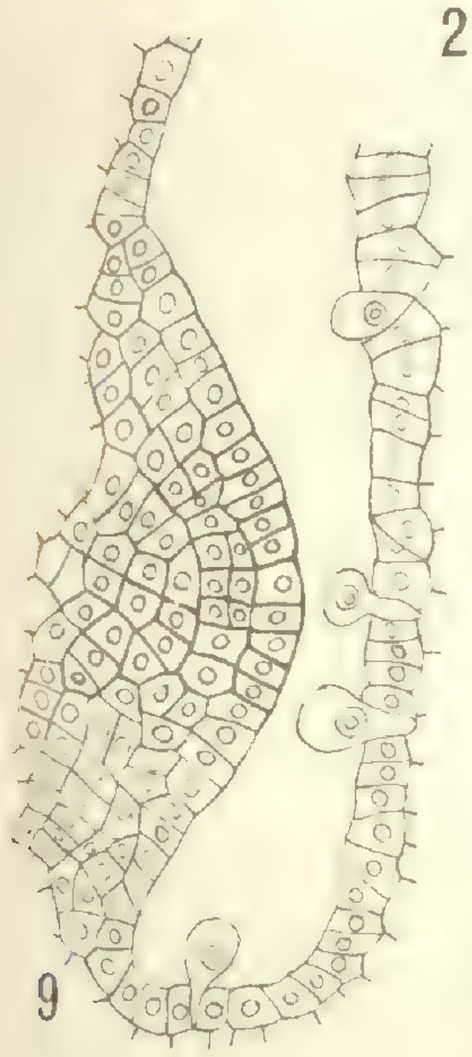
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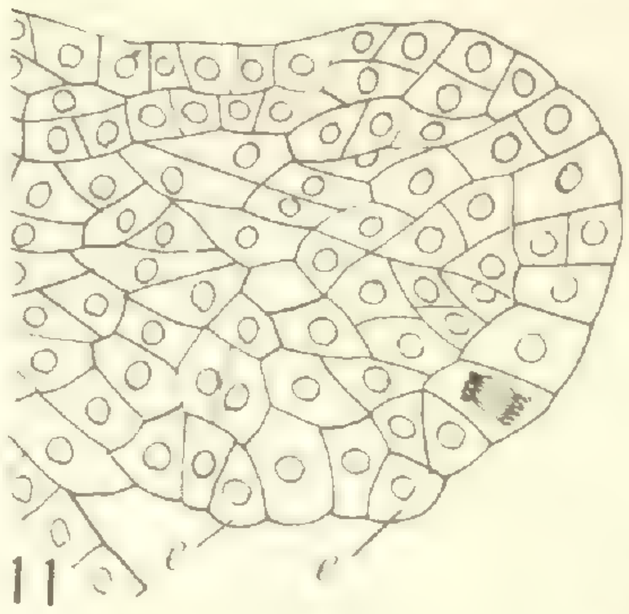
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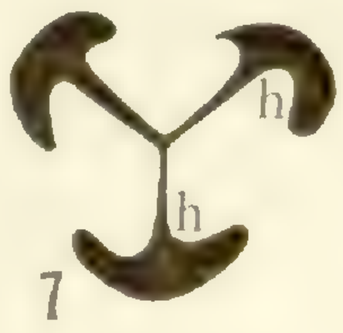

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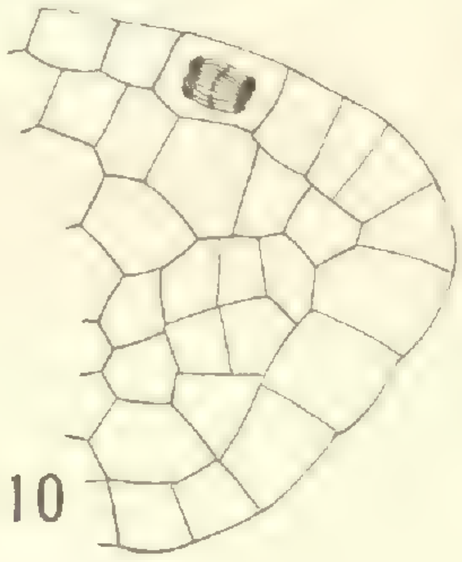
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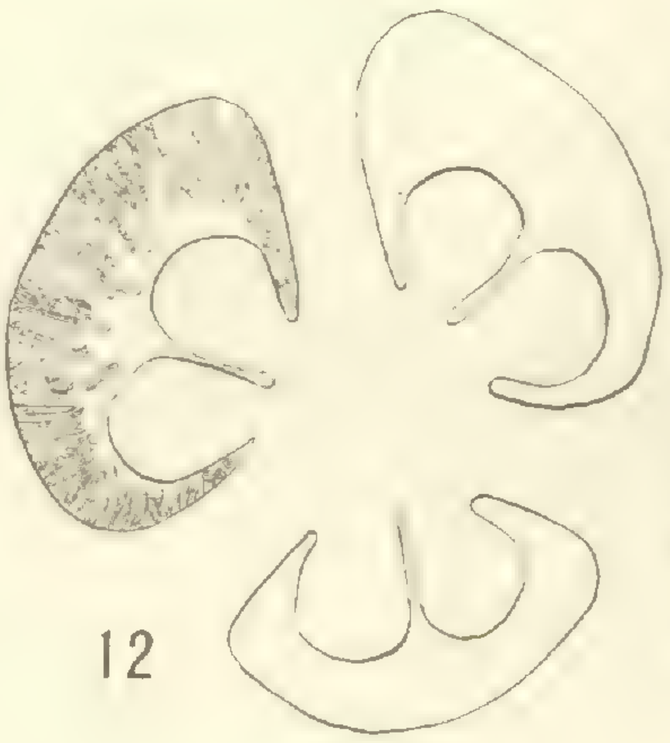
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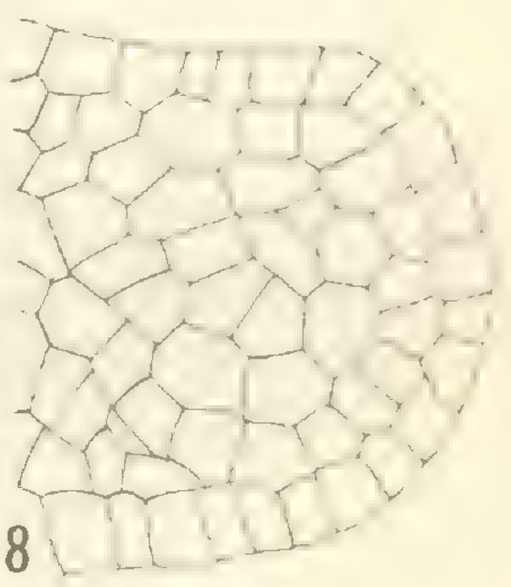
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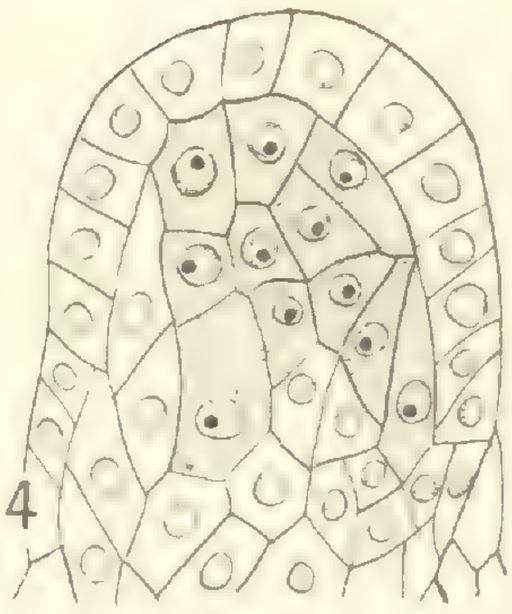
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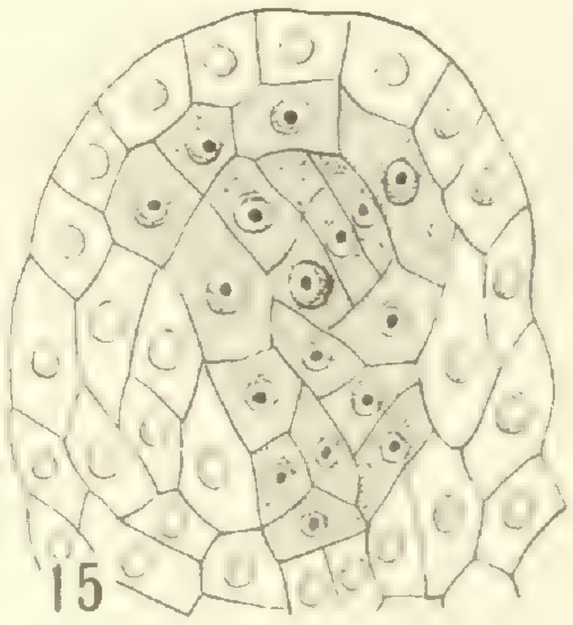
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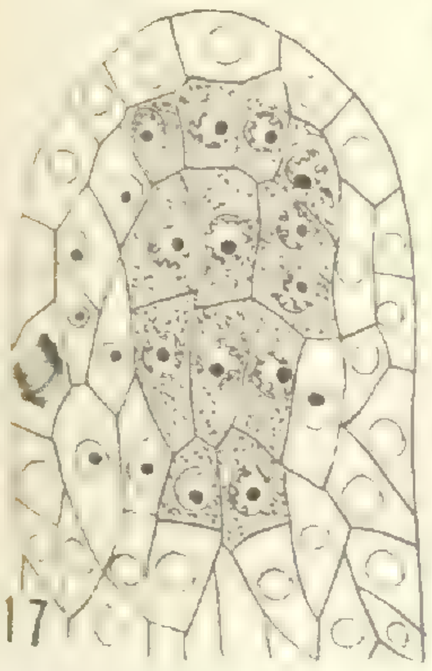
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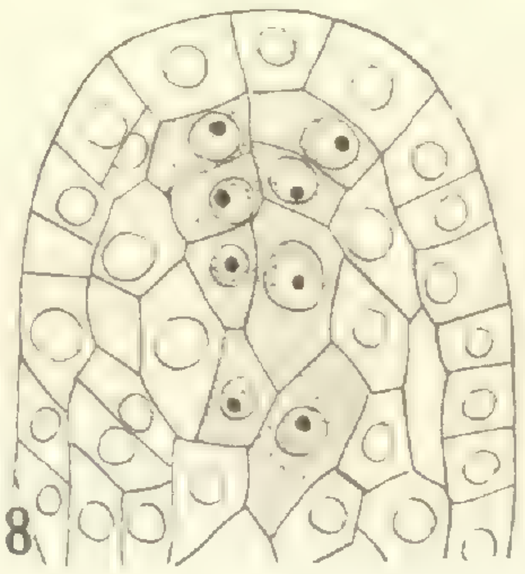
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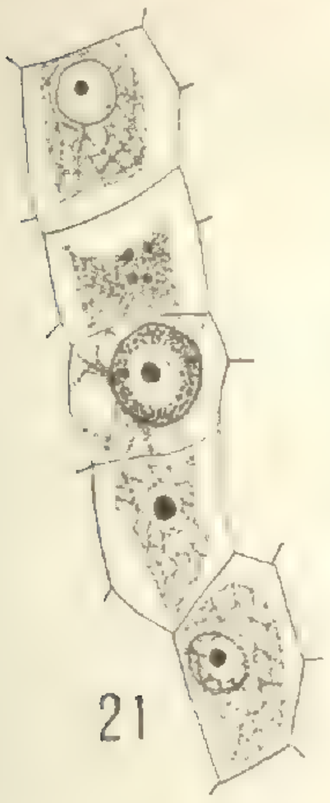

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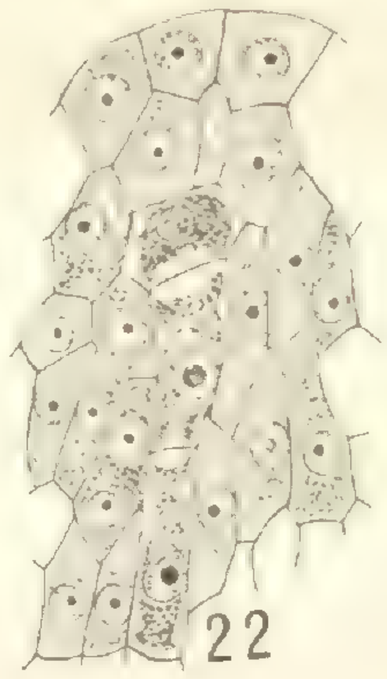

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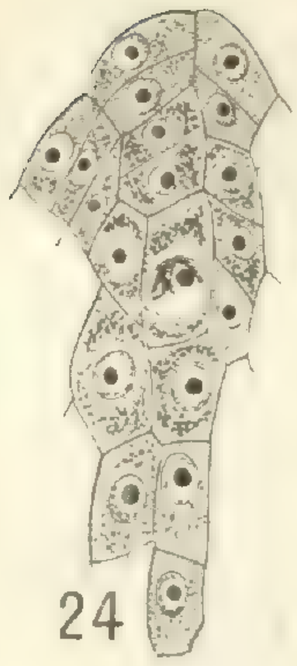

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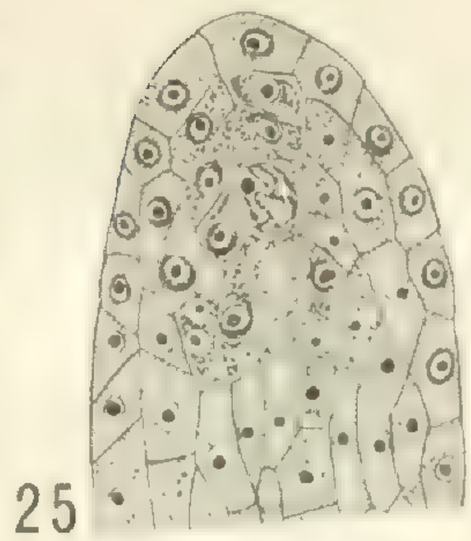

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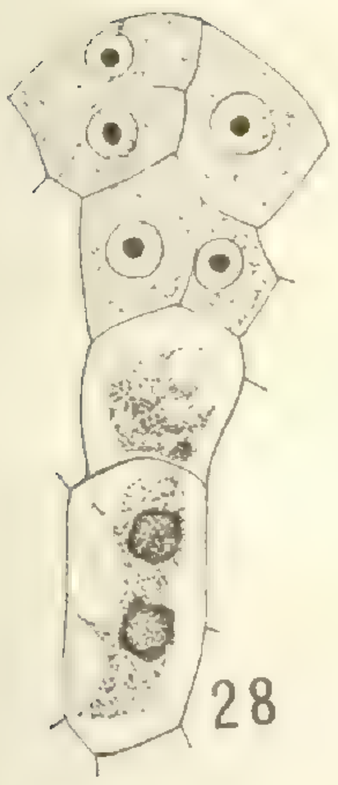

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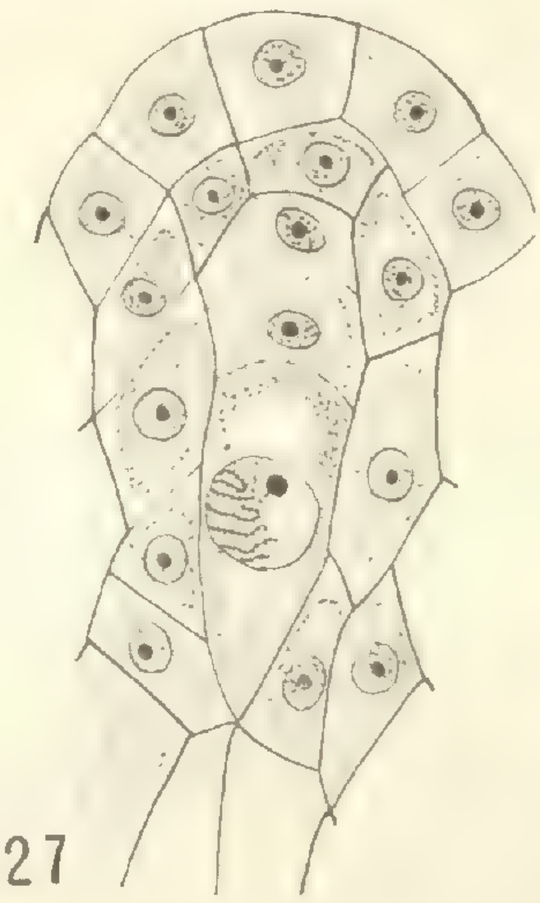

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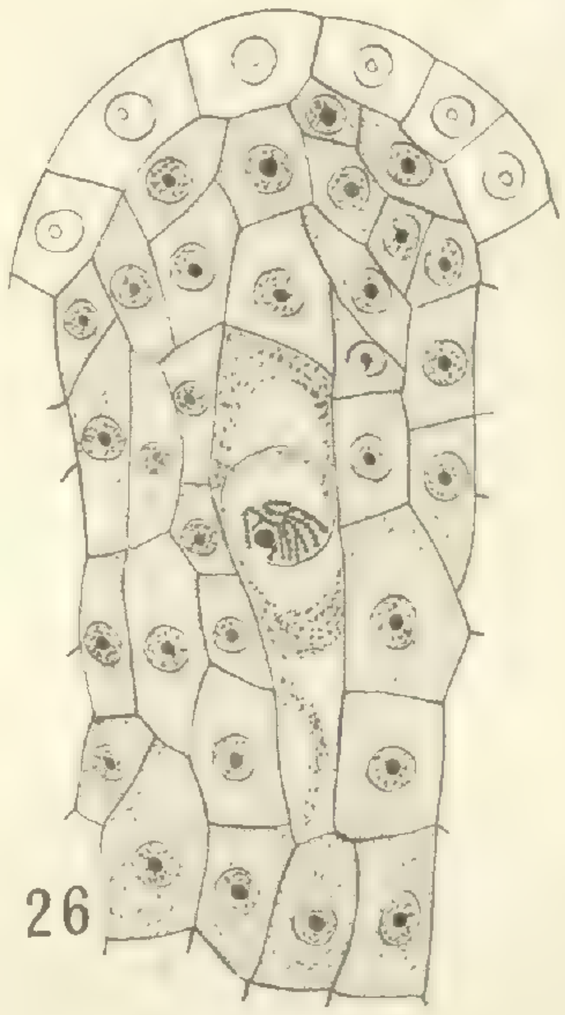

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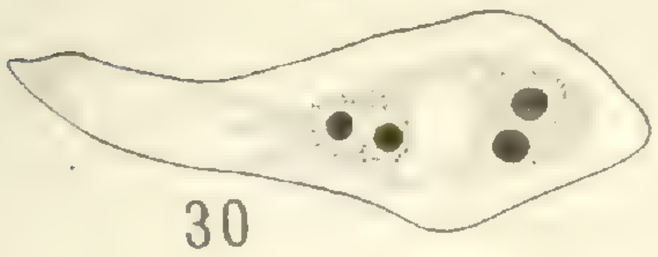

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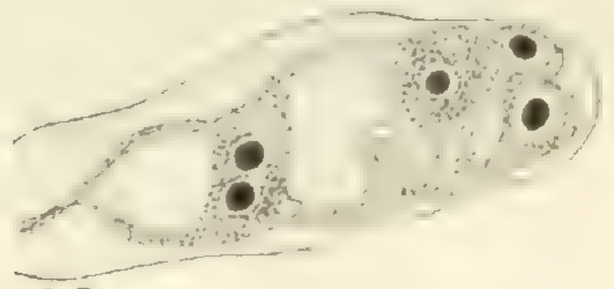

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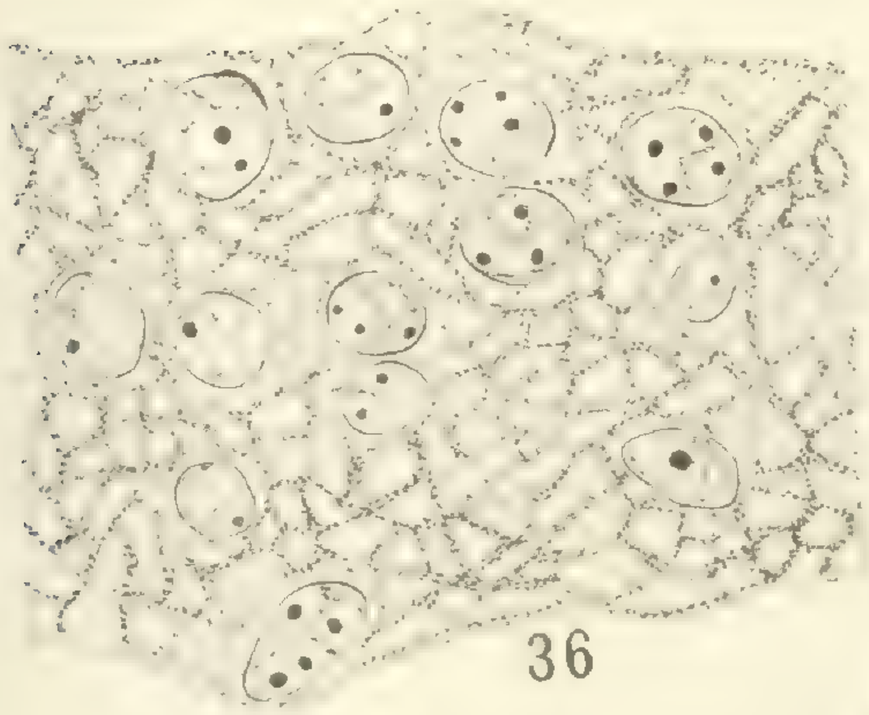

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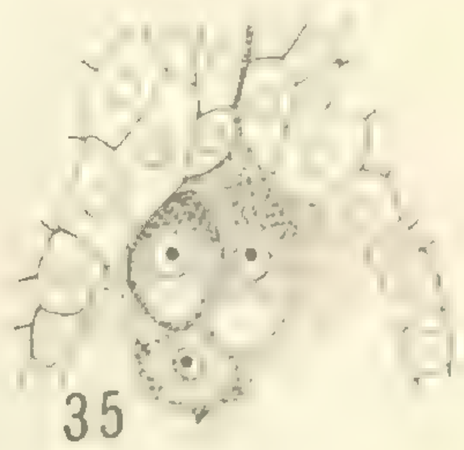

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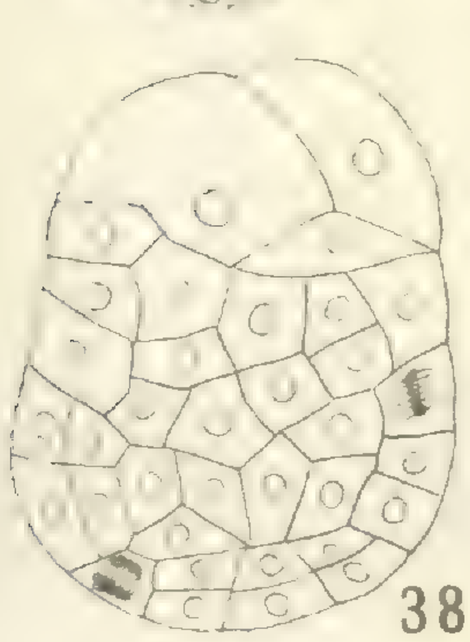

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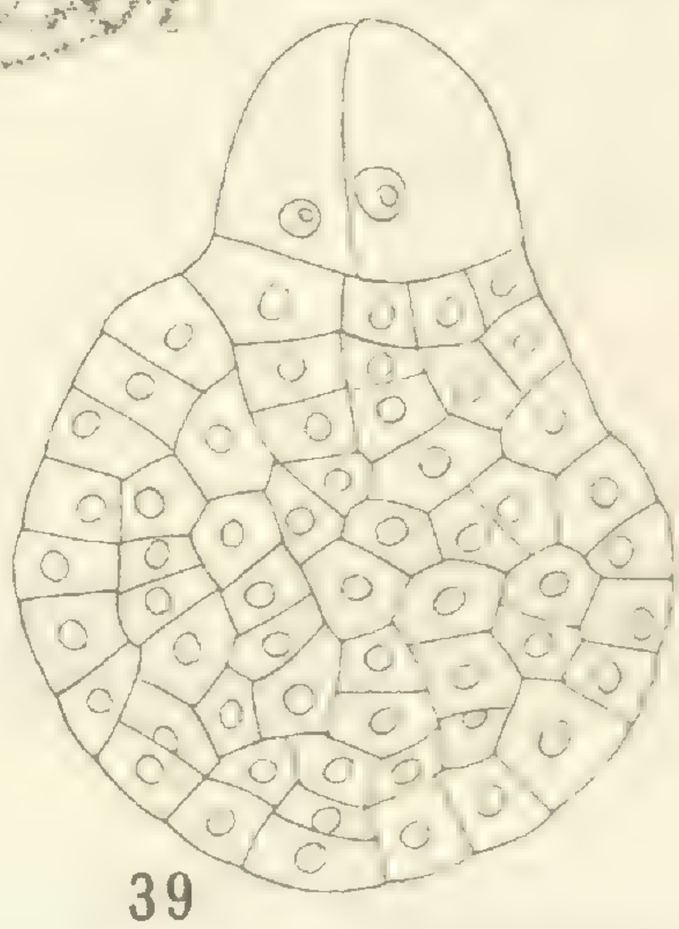

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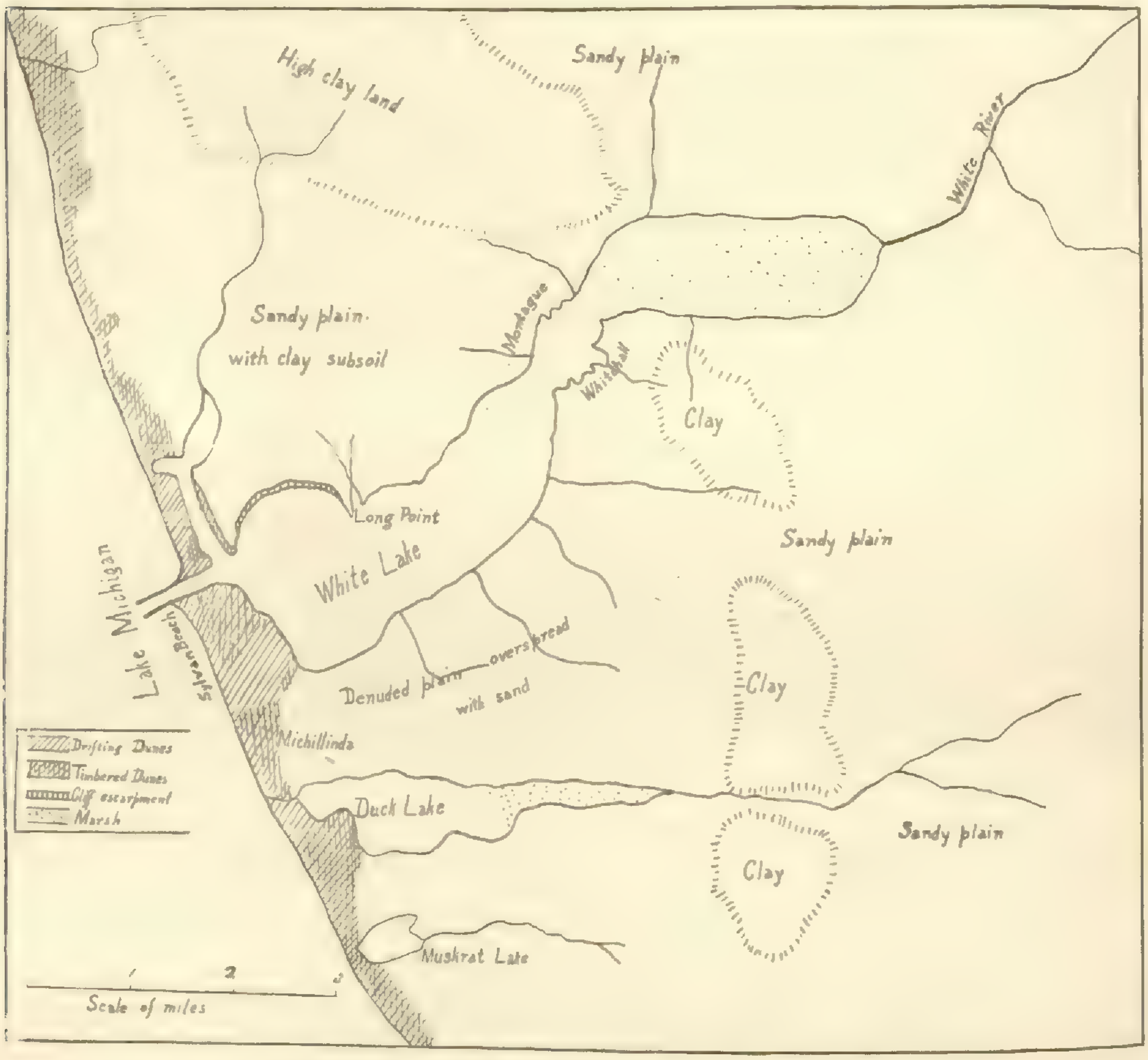
FLORA OF THE WHITE LAKE REGION, MICHIGAN, AND ITS ECOLOGICAL RELATIONS.

(WITH MAP)

E. J. HILL.

WHILE passing the latter part of August 1899 at White lake, Michigan, an opportunity was given to study the flora of the vicinity. It proved interesting in its geographical and ecological relations, and was instructive as a representative example of similar areas by the eastern shore of Lake Michigan, with which I had had more or less acquaintance in past years. White lake is one of those bodies of water, or river-lakes as they have been termed, common in western Michigan, where a stream expands into a small lake before its entrance into Lake Michigan. The river properly ends at the head of the lake where it is bordered by a tract of marshy ground abounding in reeds, wild rice, and various aquatic plants growing in the sediment deposited at its mouth and along its banks, and forming a filling which continually encroaches on the ground once occupied by the lake waters. The lake narrows again into a short outlet of river dimensions when it enters Lake Michigan. If the water of the streams forming them is of sufficient volume these lakes furnish excellent harbors, and become sites of cities and villages, while their shores are often occupied by summer cottages. They are primarily due to the geological structure of the region, dating back to the changes of level which the great lakes were subject to in Pleistocene times. Areas have been worn out by wave action, degraded by meteoric and river waters, or submerged by subsidence, which subsequently have been partly filled by sand driven in by westerly winds aided by deposits at the river's mouth. Such areas do not occur on the western shore of Lake Michigan in Wisconsin and Illinois. The eolian factor is the principal one in the filling process, and the region [is]

is consequently in its surface characters mainly a dune formation. A basin or bay-like area formed in the drift clay of the glacial period is filled with sand above the water level, the lake still occupying a portion of this area. The sand forms a dam



MAP OF THE WHITE LAKE REGION.

This map is based on one published in *The American Geologist* (1 : 143. 1888). in an article "The river-lake system of western Michigan," by C. W. Wooldridge, M.D. Only a few minor changes have been made in the portion of the map used, to indicate better some points covered by the present article.

along the shore of Lake Michigan and across the outlet of the river which impounds the water above. Doubtless the small lake owes its immunity to filling to these dunes becoming timbered before the area could be entirely filled, leaving only a river channel. Vegetation crept in from the surrounding

timbered region which lay above the level of the waters and contested the ground with the wind-driven sand until the dunes by the lake shore, becoming covered and fixed, formed a barrier against further encroachment. The surface sand washed up by the waves of the lake is now piled up on the shore dunes which tend to become higher as long as the tree covering remains as a protection. The study of the flora of such a region is important since it shows the kinds of vegetation which have this ability.

White lake is about five miles long by one to two miles wide, its deepest part being eighty or more feet. It is an expansion of White river. At the entrance of the river into the lake are two villages, Whitehall on the south side and Montague on the north. At the present outlet into Lake Michigan is Sylvan beach, a collection of summer residences, and another, Michillinda, lies just south on the Michigan shore. South of Michillinda are two similar but much smaller lakes, Duck lake and Muskrat lake. The latter is little more than a pond without a visible outlet at present, whose surplus waters must make their way into Lake Michigan by seeping through the sand. The surroundings and flora of these were likewise examined. Lying in the midst of a dune formation their shores are everywhere sandy. The region as a whole is a sandy plain with low ridges of sand more or less parallel, having a north and south trend. Moving or active dunes occur at the southwest side of White lake and by the shore of Lake Michigan. One of these lies between the old outlet of White lake and the lake shore. The natural outlet has been superseded by a short cut into Lake Michigan at Sylvan beach. The original outlet had been crowded northward by drifting sand, and ran parallel with the shore of the large lake for nearly a mile before the water escaped. This is now silted up by sand and the old outlet is a lagoon opening into White lake at its inner end.

Though this dune formation rests on a base of clay the underlying clay rarely appears in sight either by the shores of the small lakes or the contiguous shore of Lake Michigan. Sylvan beach is on a sand covered hill of drift clay, and there are low

escarpments which indicate the presence of the clay elsewhere, as along a portion of the north shore of White lake. One must go five or six miles from the lake to find the clay at the surface except near Montague and Whitehall where it appears *in situ*. The sand of the more level portion varies in depth from two or three feet to twenty-five or thirty or more, rising in low bluffs by the shores of the lake. The line of contact of the clay and sand is best shown by a series of springs along the shore and by the brooks.

This regional structure has its effect on the drainage, and by molding the hydrographic character of the basin has a corresponding influence on the flora. This differs very materially in species and distribution on the opposite sides of White lake. On the south side springs and streams are common, and the clay comes nearer to the surface, especially in depressions between the low sand ridges where the streams mainly occur. On the north side springs and streams are absent except some small ones at Montague. A large brook comes from the clay hills at the north through a rather deep valley lying between the high shore dunes and the main body of the plain, and makes its way into the old outlet of White lake that lay in the same depression. It is a perennial stream of cool water abundantly fed by springs and has the same effect on the flora along its course as does the stream-fed area to the south of the lake. Between this stream and Montague there are no beds even for storm water except near Long point where a couple enter the head of a narrow bay, now a pond and marsh, cut off from the lake by a filling of sand and saw-mill refuse. As they were dry at the time I was there, they were plainly only channels for storm water. The rain as it falls sinks into the sand and makes its way to the lake at or below the water level, or eastward toward Montague and to the perennial brook to the westward.

This indicated a drier region and a greater depth of sand. The flora was correspondingly modified. It was prevailingly xerophytic, ericaceous and arenophilous plants predominating.

On the south side it was much more varied, heath-loving plants mingling more with mesophytic kinds. In the sand plain to the north the tree covering was almost wholly white pine and oak, *Quercus velutina*, *Q. coccinea*, *Q. rubra*, *Q. alba*, and *Q. macrocarpa* being observed, while on the south side, as well as by Duck lake, Muskrat lake, and the valley to the west of the plain, these trees were interspersed with beech, sugar maple, basswood, hemlock, white elm, black ash, white ash, black birch, paper birch, silver maple, tupelo, black cherry, wild red cherry, sassafras, and white cedar. The difference was manifest in the color of the corn in the fields and the behavior of the grass. On the north side the corn was pale and the grass with difficulty made a sod; on the south side the corn had a deeper green, but not the rich green color which comes from a deep firm soil, and the grass sodded fairly well in damper places. But wherever there was a bare surface, as in plowed fields and roadways, the ground showed a sand plain.

The floral societies formed by this mixture did not readily harmonize with ideas of plant ecology based on experience with plants growing in a soil more natural to them and under conditions more uniform. I was familiar with this in the dune region at the head of Lake Michigan, where the herbaceous vegetation is much varied and the arboreous considerably so, but the tree covering south of White lake much exceeded it in variety. It was a surprise to find on the top of a dune, or sand covered hill with a base of clay like that on which Sylvan beach is located, a comparatively pure beech wood. The hill is capped with sand blown up from the neighboring beach. Its south end to some extent still battles with the winds, and owes its immunity in part to their prevailing direction from the northwest, which makes their work more effectual on the north end of the dunes lying toward Michillinda. These dunes, together with the sand washed up in the low interval between, furnish the material of the large active dune now encroaching on White lake. The timbered dune between this opening and Michillinda is high and steep on both sides. Within the space

of a few square rods on the top bordering the part against which the wind was acting I made a list of the following species: beech, sugar maple, red oak, black cherry, hemlock, white pine, white cedar, common juniper, witch hazel, poison ivy, two dogwoods (*C. stolonifera* and *C. Baileyi*), and the willow, *Salix glaucophylla*. On the ground the lesser growth was composed of *Pyrola secunda*, *Arctostaphylos Uva-ursi*, *Polygala paucifolia*, *Aralia nudicaulis*, *Campanula rotundifolia*, *Mianthemum Canadense*, and *Solidago caesia*. The list of herbaceous plants could have been easily increased by walking about a little, but I purposely sat down so as to make a list in sight from a single point of view as a limitation. This was on a narrow crest of sand with a steep timbered slope to the south, and a still steeper one of bare sand to the north extending down to the low area of moving sand a hundred or more feet below. It was possible for all this variety of vegetation to be in time blown away, though the work of the wind was slow, for there was evidence at hand of what it had already done. It was also plain that the plants grew in a soil of sand so little compacted as to be easily moved by the wind when once the covering had been removed.

In the sand plain north of the lake the herbaceous and shrubby flora was less diversified but still well represented in species. Where the oaks prevailed the tree covering was quite open. There were dense groves of young white pine, for the old trees had nearly all been removed to the sawmill. From the stumps which remained it was seen to have been a mixed forest of pine and oak at the time the trees were cut. The undergrowth varied according to the density of the tree covering and somewhat according to its kind, whether of oak or pine. The common wintergreen, the pyrolas, and pipsissiwa were more generally found under the dense growth of pine. The usual ericaceous plants were *Epigæa repens*, *Arctostaphylos Uva-ursi*, *Gaultheria procumbens*, *Pyrola secunda*, *P. chlorantha*, *P. elliptica*, *P. rotundifolia*, *Gaylussacia resinosa*, *Vaccinium Pennsylvanicum*, and *V. vacillans*. In somewhat more fertile areas or deeper humus soil *Monotropa uniflora* was frequent and *M. Hypopitys* was detected

once. The fringed polygala was also frequent, generally in company with the trailing arbutus, which was very abundant, and together they must have made a fine floral display in early May. The polygala occurred under quite different conditions south of the lake, for besides on dunes and the drier sand plain it found a home in the damp sand as a companion of such plants as *Clintonia borealis* and *Trientalis Americana*. *Vaccinium Canadense* also accompanied the other huckleberries in moister areas south of the lake. In the dry plains both north and south were great quantities of *Comptonia asplenifolia*, sometimes quite exclusive of smaller growth. *Pteris aquilina* was equally abundant in spots but not covering such wide spaces as the *Comptonia*. It was the only fern observed in the dry sand plain. *Rhus copallina* was the most common sumach, often much dwarfed and flowering when a foot or less in height. *R. aromatica* and *Shepherdia Canadensis* were frequent along the bluff shores of the lake and occasionally were seen elsewhere in the woods. The most frequent papilionaceous plants of the season were *Lespedeza polystachya* and *L. Stuvei* var. *intermedia*, *Desmodium paniculatum* and *D. nudiflorum*, the latter often under the pines with the pyrolas. The sunflower was chiefly represented by *Helianthus divaricatus*, slender, often dwarfed, and bearing small heads barely an inch in diameter. *Liatris scariosa* was the common blazing-star. The principal goldenrods were *Solidago hispida*, *S. juncea*, and *S. nemoralis*; and the asters mostly *Aster corymbosus*, *A. azureus*, and small forms of *A. laevis*. The round-leaved orchid, *Habenaria Hookeriana*, occasionally occurred, and more commonly *Lycopodium complanatum*.

These were the most typical plants seen in the wooded sand plain north of White lake, a list by no means exhaustive even for the time of the year, but representative of the flora. Nearly all of them were met with on the south side, commonly on the dry sand ridges, and helped to give the flora south of the lake a more mixed and diversified character.

The cool brooks fed by springs, the springy and swampy places south of the lake, had a tree growth in which the white

cedar, black ash, hemlock, cherry birch, paper birch, and white pine were variously intermixed. *Alnus incana*, *Cephalanthus occidentalis*, *Ilex verticillata*, *Pyrus arbutifolia*, *Rosa Carolina*, *Salix discolor*, and *S. cordifolia* were the more common shrubs. The damp shaded reaches along the streams showed such plants as *Mitella nuda*, *Mitchella repens*, *Cornus Canadensis*, *Clintonia borealis*, *Trientalis Americana*, and *Habenaria psycodes*. Here the ferns obtained the proper conditions of growth and occurred in considerable variety. The most frequent were *Aspidium Thelypteris*, *A. spinulosum*, *Osmunda cinnamomea*, *O. regalis*, *Asplenium Filix-foemina*, *A. acrostichoides*, *Onoclea sensibilis*, *Phegopteris Dryopteris*, and *Adiantum pedatum*. Some of these, especially the last two, occurred in the drier area of beech woods along with the Pteris, though this was more abundant in the oak woods. The most interesting fern of the swampy ground was a *Botrychium ternatum*. It was abundant in a locality where the tupelo grew, and where the ground was also closely shaded by a larger fern, *Osmunda regalis*. The botrychiums were from three to twelve inches high, some so hidden that the fronds of the osmunda had to be pulled aside to find them. It was a peaty soil mixed with sand, so charged with humus as to be quite dark colored. Some grew on the hummocks made by the matted roots of the osmunda, the roots of the two ferns being interlaced, but they were more frequently seen in bare spaces between the hummocks, which in the early spring or rainy season must have been quite wet, or even have had water resting on them for a time. Some were growing in soil principally made of the much decayed remnants of a fallen tree. In all conditions it was a soil of a strongly humus composition. This was a surprise to me, for in all previous collections or examinations of this fern the soil had been clay, often a rather stiff clay-loam, or sand as in the dune region east of Chicago. Finding the tupelo led me to search for another plant which I have quite generally found associated with it, *Bartonia tenella*. It was soon discovered on the little hummocks made by ferns, mosses, and other plants, or on abandoned ant hills beneath the trees. The association seems more than casual but may only be due to soil conditions.

The immediate shores of White lake differed considerably in the character of the flora on opposite sides. On the north side was a flat strip of sandy ground, slightly above the level of the water and lying between it and the bluffy shore. It was low enough to be subject to wave action when the winds were strong, or to freshets when the water of the river was high. Here shrubs were scarcely seen, the plants being those of wet sand and shallow pools. *Lobelia Kalmii* was very common. Other representative plants were *Gerardia purpurea*, *G. paupercula*, *Spiranthes cernua*, *Parnassia Caroliniana*, *Juncus Balticus*, *J. Richardsonianus*, and *Carex viridula*. In the shallow pools *Proserpinaca palustris* and *Potamogeton heterophyllus* occurred, the last becoming terrestrial by the drying away of the water. There were similar strips on the south shore, but between the immediate shore and the bluff there were often areas of swampy or boggy land overgrown with willow, alder, and white cedar, dense thickets which showed the influence of the adjacent springs, or of water seeping out from the banks above the clay.

The active dunes had the scanty flora so characteristic of those about Lake Michigan. The plants observed at White lake were mainly *Calamagrostis longifolia*, *Cakile Americana*, *Euphorbia polygonifolia*, *Corispermum hyssopifolium*, *Cardnus Pitcheri*, *Solidago Virgaurea* var. *Gilmani*, *Salix adenophylla*, *S. glaucophylla*, *Cornus Baileyi*, *C. stolonifera*, and *Prunus pumila*. As the advance of the dune was very slow the shrubs and perennial plants were not infrequent on the windward side among the annuals much above the base of the dune, showing the ability of the seed to sprout and take root in the sand much exposed to wind action. In fact the favorite place of *Cardnus Pitcheri* is everywhere on the windward side of a wind-swept area.

In the lower area of the active dune region lying between the southward bend of White lake and the shore of Lake Michigan, the two above mentioned willows were accompanied by *Salix longifolia*. Here, as frequently elsewhere along the shore, *Salix glaucophylla* had very small much thickened leaves an inch or two long by half an inch or less wide. *Hypericum Kalmianum*

was a common shrub of the locality. *Aster polyphyllus* was abundant and was also seen in higher ground south of the lake. *Cladium mariscoides* occurred in wet places, and several of the plants that have been mentioned for the low sandy borders of the north side of White lake. *Utricularia cornuta* occurred in pools. It was a small sand plain with shallow depressions and low dunes, bare or partially covered with vegetation, an area in which was to be seen a struggle with the destructive winds and a partial success in recovery.

In the deep valley of the brook which joins the old outlet of White lake some interesting forms and associations of plants were found. The white cedar was the common tree in the springy ground. Rills fed by springs along the eastern slope were frequent. Two club-mosses, which are ordinarily seen growing in different societies, were here in company, *Lycopodium lucidulum* and *L. annotinum*. Such a locality is natural to the former, but the latter is usually a denizen of drier grounds, and was here seen in company with *Medeola Virginica*, *Trientalis*, *Clintonia*, and *Viola Labradorica*. The eastern slope was scarped out of the pine plain and was densely covered with white pine and hemlock; the western was made by the high and fixed dunes which form a narrow range between the valley and Lake Michigan, with a flora similar to that of the high dunes south of White lake. In one of the quieter places of the rills a semi-aquatic or floating form of *Marchantia polymorpha* abounded. Some rested on dead leaves and twigs lodged in the water. They were not attached by rhizoids like the ordinary terrestrial form of this liverwort and could be lifted out of the water by the handful like a Lemna or a floating Riccia. The thallus was very thin, especially near the base, the thinnest parts formed of the lower series of cells which enter into the structure of the thallus, the upper or lozenge-shaped layer with the stomates being absent or prevailing in the distal portions. At first it seemed distinct, but the occasional presence of the characteristic cups and gemmules, and the structure as a whole, showed its affinities with the ordinary form found on adjoining logs and earth from which it had spread into the water.

Duck lake is similar to White lake but much smaller. Its southern shore is considerably higher than the northern. The water is clear and quite cool, being well supplied with springs and having only a small stream entering its head. There is a narrow belt of moving sand lying between it and Lake Michigan. To the south are high dunes, skirting the Michigan shore between it and Muskrat lake. The upper end is very reedy, and there is an abundance of aquatics in its shallow parts. In White lake I had found the usual potamogetons to be *P. pectinatus*, *P. perfoliatus* var. *lanceolatus*, *P. lonchites*, *P. amplifolius*, and *P. heterophyllus*. These were also common forms in Duck lake together with *P. natans*, *P. zosteraefolius*, and *P. Robbinsii*. The last had not reached the stage of mature fruit, which is in September and October, but was well provided with flowers and young fruit. This was interesting because it showed that the species may fruit under such conditions as potamogetons ordinarily do. It is usual to find the stems barren, and they are generally said to fruit, if they fruit at all, in shallow water or when ponds in which they grow partly dry up. This was the case in the only locality where I had previously found it fruiting freely, the Chesago lakes, Minnesota. It is very abundant in some of the small lakes of northern Illinois, where the stems are mostly from one and a half to two or three feet long and very leafy. In Duck lake they were less leafy as a whole, the fruiting stems four to six feet long, as this was about the depth of the water. They were rising and bringing the inflorescence to the surface of the water, or near to it, like *P. pectinatus* and the others with which it grew. All were flourishing equally well in the dark ooze which overspread the bottom where they stood, and according to their season were equally well provided with fruit or the promise of it. Nor was there any evidence of the shallowing of the water, except the contrast between summer and the rainy season, not very marked in a lake of this character fed by springs.

The high dunes to the south of Duck lake had on their slopes frequent patches of the yew, *Taxus Canadensis*. On the north slope of one whose base is washed by the waters of the lake it

was a surprise to find *Polypodium vulgare* growing on the sand of the hillside under pines and hemlocks and closely associated with the yew. The beech stood close by. It was strange to get the polypod, the yew, and the beech-drop (*Epiphegus Virginiana*) growing in the same sandy soil and near neighbors. The fronds of the polypod were fine fruiting specimens from three to twelve inches high. It was the first time I had met with it except on rocks. *Aspidium marginale* was likewise a frequent fern on the slope of the hills. It attained a very luxuriant size in the depressions among them, where fronds three feet high were measured. This fern was also common on the east or wooded side of the dune lying between the old outlet of White lake and Lake Michigan, growing here also with the yew under the pines and hemlocks.

South of Muskrat lake is a large fine tract of primitive forest as yet but little touched by fire or the woodman's axe. It is on a sandy, gently undulating, or in places almost level, plain. It is known as the "beech woods," as these trees abound and fine examples of them occur. Being dense the undergrowth was not extensive, but like that of the denser woods lying between White and Duck lakes.

Once I met with the cancer root, *Conopholis Americana*, but the abundant parasite, so-called, in all such woods is *Epiphegus Virginiana*. It is closely associated with the common beech, but I do not succeed in making out any very definite connection between it and the roots of the beech tree. As regards the soil the bulbous or thickened base of this plant is very superficial in position. Some of them have finer roots which run deeper, but the short, simple, or branched organs which cover the surface of the bulb and give to it its rough exterior do not have a root connection. They point in almost all directions and are often found springing from the stem above the place where the scaly leaves appear. The tip of these organs is slightly enlarged, of open tissue without epidermis. There is no similarity here between this and the strong union, or large haustorium, one finds in the case of the allied broom rape, Conopholis, and its host

tree, which I have found to be the oak, or in one case a hickory, and in which the parasitism as seen in section reminds one of that of the mistletoe. There are dozens of these organs on the bulb-like base which lies among the leaves and the humus made by their decay and must be in close contact with them on every side. A saprophytic relation is forcibly suggested, and one connected with beech leaves rather than with the roots of the beech, for the association is always with the beech tree. The leaves have an acid flavor and the wood is one of the best to yield wood vinegar by destructive distillation. The fresh seedlings of the beech, also called beech drops, are pleasantly acid to the taste, and their large cotyledons are eagerly eaten by children as they come up in the spring. It is possible that there is in the beech leaves or the mold made by their decay something which suits the nature of the Epiphegus.

Quite frequent in the beech and oak woods was a mycorhizal plant, *Corallorhiza multiflora*. Its mass of toothed, coral-like roots are buried much deeper in the soil than the bulb of the Epiphegus, sometimes to the depth of two or three inches. Many fine examples of these were seen, some with paler, yellow scapes and flowers, the color reminding one of *C. innata*.

Two introduced plants found in the outskirts of Montague proved of special interest. *Gypsophila muralis* was growing in the dry sand of a little used street. It has the habit of *Arenaria patula*, but a habitat more congenial to *A. stricta* as seen about the great lakes, for I have met with the former only on the thin soil of limestone rocks, where it may be accompanied by *A. stricta*, a common plant of the dune region of northern Indiana. The other immigrant was *Sedum acre*. It formed dense patches by the side of the street and had spread into the adjoining woods, closely covering the ground like a mat, and making an excellent sand binder, green and turfy looking. It was occasionally seen in other places about White lake. As a rock plant I have found it in Illinois in company with *Arenaria patula*.

The physical conditions about White lake and similar tracts of sand-filled depressions along the eastern shore of Lake

Michigan furnish fine illustrations of the ability of plants, and especially trees, to spread from an area where the conditions of growth are more favorable to one where they may be much less so. They emphasize the plasticity of plants. The species may suffer in vigor of growth and have a much less bulk, but they usually fruit very freely, often surprisingly so. At White lake was a basin filled with sand surrounded and underlaid by drift clay, or by materials that enter into the drift formation and on which in our latitude the mixed forests of deciduous species mainly occur. North of the lake, with its deeper and drier sand, the oaks were almost the only kinds to come in and compete with the white pine. South of the lake, where there was more dampness and a nearer approach of the glacial drift to the surface, except on the high dunes, and a more marked tendency to a loamy condition of soil, there were many more kinds of trees and herbaceous plants to share the ground with the pine. But the trees best adapted to a clayey soil not only crept across the area of low sand ridges and the intervening and more favorable hollows but passed up and appeared in force on the high dunes along the Lake Michigan shore, just as they may be seen on a narrow strip of dunes superposed on the clay of the lake shore, where a hardwood forest closely abuts it without any sand-filled basin to the eastward.

I have been struck repeatedly by the distribution of some of the deciduous trees of dune regions, such as that at the head of Lake Michigan in Indiana and Illinois. The basswood is one of the best examples. It appears eastward in the area of broken or active dunes where it is practically confined to a narrow belt by the lake shore and to a similar belt further south along the Calumet river. It frequents the more protected slopes of dunes or hollows lying between neighboring sand hills, though like other trees, from the shifting character of this portion of the dune region, it may be so situated as to give the appearance of growing originally on a crest. West and south it appears again in the area of low sand ridges and shallow lakes and ponds where the conditions are more like those of forest

strips or islands of the prairie region, where it is accompanied by such trees as *Quercus bicolor*, *Q. rubra*, and *Q. acuminata*, additional to the common black oaks which are spread throughout the dune region. Other trees are the hackberry, white elm, tulip tree, shagbark and bitternut hickories, white ash, blue ash and some kinds of Crataegus. Most of these are common trees on the drift clay to the south and west, and all appear somewhere on the bordering clay-land forests, but are scarcely seen in the area of broken dunes, except an occasional red oak, some white oak and bur oak or a bushy form of the Celtis specifically distinct (*C. pumila* Pursh). Lying between these two sections is a strip where the basswood as well as these other trees is absent. There would seem to be sufficient moisture at least, for it is mostly a region of low sand dunes, parallel sand ridges, and intervening sloughs, the ridges with a prevailing heath vegetation. It is the home of the gray pine (*Pinus divaricata*), sometimes almost exclusively so. Where the white pine prevails or shares the ground more freely with the gray pine, the basswood comes in. This is a common tree of the forests to the eastward of these dunes in the drift covered areas, together with the sugar maple, beech, tulip tree, and various other kinds. But nearly all except the basswood and the oaks cease in the belt of less pure sand or sandy loam, lying between the dunes proper and the clay region. There may be in the basswood peculiarities of structure or physiological adaptations better fitting it for xerophytic conditions than the others when they move away from such as are suited to mesophytes. Its leaves become much thicker than when growing in its usual home. There is in the fruit one advantage for more effectual dispersion, the ligulate bract attached to its peduncle, which in a strong wind helps to carry it to quite a distance from the parent tree. Most of the trees which formed the mixed forest to the south of White lake, and like the basswood showed this ability to spread away from a contiguous region more congenial to them, not only fruit freely but have a heavy seed, which, when lying on the surface of the ground, is not easily displaced. Such seeds sprout quickly in

the spring when there is most moisture and when the temperature is moderate. Being well provided with food stored within their coats they can carry on the processes of vegetation till the seedling is well rooted. Thus being more independent of external conditions they have an advantage in establishing themselves in a less favorable environment, such as that of dry sand.

In considering the vegetation of dune areas, especially those of the "Michigan sands," such as appear by White lake, we must also bear in mind that some of them are comparatively well provided with alkaline earths, that all have some amount of these or there would be no tree growth at least. They often produce abundant crops of fruit, especially of kinds that do best in light soil, like the peach. The prevailing constituent of the soil is silex, but microscopic examination and chemical tests show that feldspar, mica, pyroxene, and other minerals are present, such as contain potash, soda, lime, and magnesia, the most important of the alkaline earths. The pebbles of the shingle along the beach are a mixture of various kinds, quartz prevailing, but feldspars frequent, with some limestone. This must be the case since they are mainly produced by the degradation of drift material. The comminuted sands formed from them must necessarily contain the same ingredients, though the harder, coarser, and more resistant quartz sand will be most conspicuous to the eye as well as most abundant. The percentage of ash in the wood of such trees as form the principal covering of a dune region is relatively small. As seen in the analysis reported in the volume of the Tenth Census on the forest trees of North America, the pines have an average range of .19 to .23 per cent. The two most common oaks, *Q. velutina* and *Q. coccinea*, have .28 and .19 per cent. respectively. The white oak and the bur oak are higher but are much less common trees. The leaves and bark would show a higher percentage, but as they fall and the trees decay this is not only restored to the soil but they take with them other important ingredients which enter into the composition of humus. The beech, sugar maple, basswood, hemlock, and some other forest trees likewise stand considerably

higher than the pines and the most common oaks in their percentage of ash, but they, too, are much less common, often wholly absent from large areas. In general, analyses seem to show a smaller percentage of ash in the same species when growing on sandy or gravelly soil than on soils stronger in such mineral ingredients as the trees use, like clay, clay-loam, or lime soils.

But alongside of mineral constituents certain physical conditions are equally important or indispensable. The ability to reach and appropriate what is provided must exist. Porosity, depth of soil, moisture, here come into play. The last is the most important of all in soil conditions, since vegetable life is impossible without some degree of it. For porosity sand ranks the highest, in capability of retaining water it is the lowest, clay being the highest; in capacity for condensing moisture from the air, it is likewise the least powerful, humus and clay being best. In discussing such matters as these, Schlich well states what must have become evident to any who have made a comparative study of the vegetation of the dunes and of the bordering region. Though written with reference to cultivated woods it is as true of the natural forests. "Woods thrive equally well on soils of the most different geological origin, while great differences exist in the development of the same species if grown on soils of the same geological origin. The phenomena are explained by the great importance of the physical qualities of the soil, depth, porosity, and a proper degree of moisture"[1] These conditions go far toward explaining the differences in vegetation seen on the opposite sides of White lake and in corresponding regions, for they are true of vegetation as a whole as well as of the trees. In the case of the trees it was a "mixed wood," but a "mixed wood" of much greater variety on the south side where the physical constitution of the soil as well as its chemical ingredients furnished a more suitable habitat. Though it was throughout a dune formation superposed on a clay substratum, the relations of the vegetation to the substratum were also most

[1] Manual of Forestry 1 : 143. 1889.

favorable on the side of greater mixture. For the roots together with the greater supply of moisture took with this in solution the ingredients which existed in greater abundance in the comminuted soil itself. These beneficial relations also made the forest conditions more favorable in another way, and helped to perpetuate them, as they continually added to the humus, for this was much more in evidence on the side of the greater mixture.

CHICAGO, ILL.

BRIEFER ARTICLES

PHYSIOLOGICAL NOTES. II.

(WITH THREE FIGURES)

3. An artificial endodermis cell.

Since the osmotic pressure depends upon the impermeability of the "semi-permeable" membrane to the solute, it is possible for the osmotically active matter in a cell to exert a different pressure in different directions if the protoplasm is permeable to it in different degree in different parts; and by exerting different pressures it should,

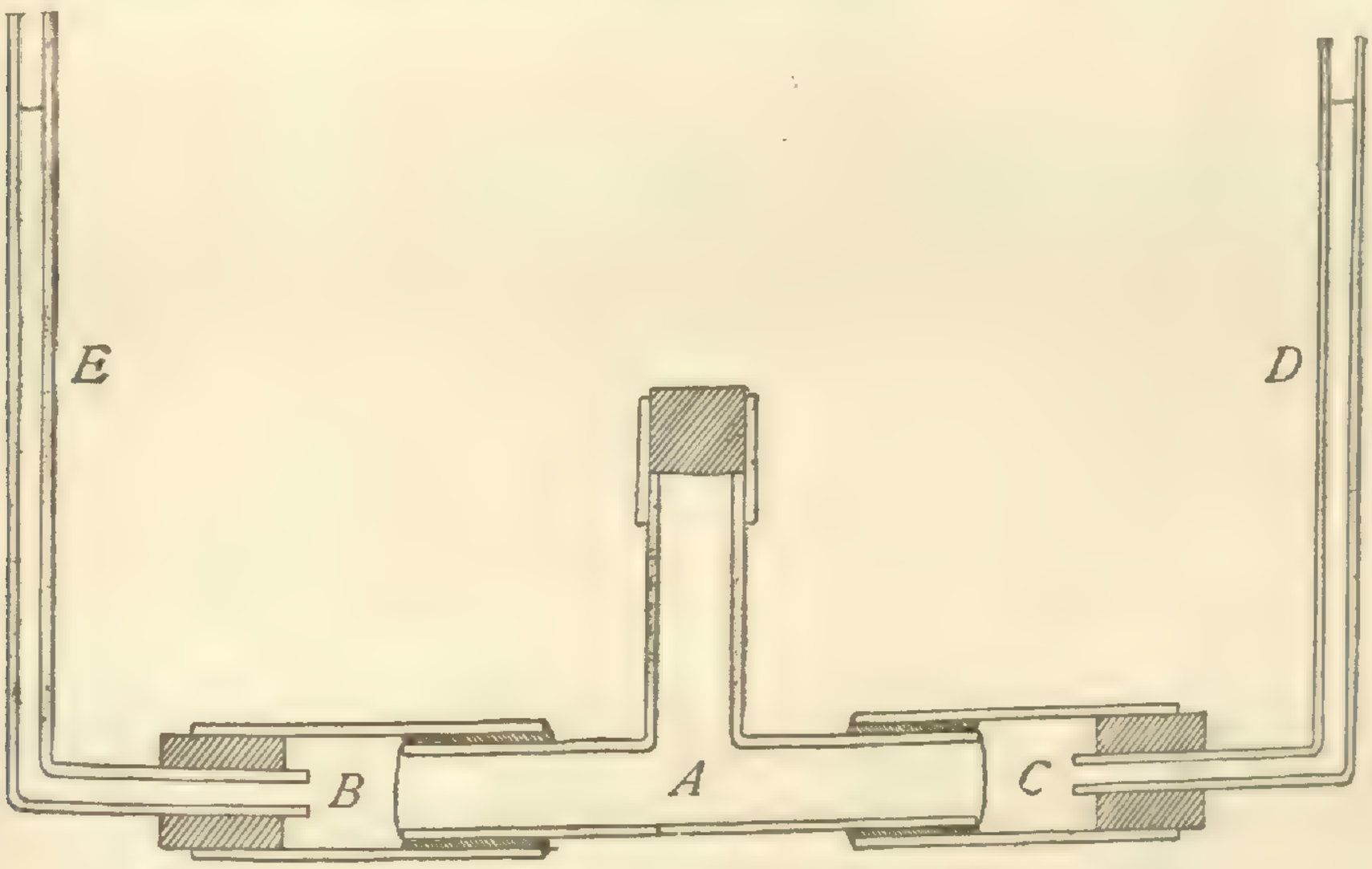


FIG. I.

when in a state of complete turgescence, take up water where the semi-permeability is most perfect, and pass it off where the pressure is least. This is generally accepted theory, though its clearness may depend somewhat on the reason given for the entrance of the water, but its soundness has not hitherto, so far as I know, been demonstrated experimentally. This may be done as follows: over two ends of a T tube *A*, tie parchment paper; soak one of these ends thoroughly in a solution of $K_4Fe(CN)_6$; seal both ends into glass tubes, *B*, *C*, with communicating tubes, *D*, *E*, bent at right angles, fill the tubes *C*

and *D* with $K_4Fe(CN)_6$; fill *B* and *E* with distilled water, taking care that the liquids stand at the same height in *D* and *E;* fill *A* with $CuSO_4$, and close it. The membrane containing $K_4Fe(CN)_6$ is promptly filled with a precipitate of $Cu_2Fe(CN)_6$ which is practically impervious to $CuSO_4$, and any leak in this precipitation membrane will be immediately mended. The other membrane, of parchment paper alone, is relatively easily passed. The pressure against it is accordingly less. I have worked the experiment using 6 per cent. $CuSO_4$ and 3 per cent. $K_4Fe(CN)_6$. After 2 hours 15 minutes, the $K_4Fe(CN)_6$ column had fallen 1^{mm}, and the column of water had risen the same distance. Wishing to stop while the water was as pure as possible. I poured it out then, and was unable to detect any copper in it with $K_4Fe(CN)_6$; it may have been there in extreme dilution, or it may have passed into but not yet through the membrane. What had been done then was taking water out of a solution of appreciable osmotic strength, and forcing it over into practically pure water. The energy to perform this work is furnished by the loss of $CuSO_4$ from the T tube, as is easily seen if the experiment is continued longer. The concentration of the solution that is forced through the parchment membrane must obviously be at first slightly in excess of that of the $K_4Fe(CN)_6$ that the water is drawn from.

The experiment is interesting in botany, because root pressure must be caused by exactly this same process. Under certain very unlikely conditions, differences in temperature, without any loss of dissolved matter, might cause guttation, but they could not cause root pressure, because all parts of the root must be at too nearly the same temperature. That any sort of "pulsations," without variations in the resistance to the escape of the solute, could cause root pressure, will appear impossible until some adequate source of energy is shown, and if the solute escapes it is unnecessary to imagine rhythmic or any other variations. As Pfeffer suggests, pure water might be forced from a cell by local internal differences in concentration, but it would require energy whose source is unsuggested, to set up and maintain these differences.

In order that root pressure may be caused in the way that the experiment with this artificial cell illustrates, the protoplasm must be permeable to the osmotically active matter of the cell sap in different measure in different parts of itself — which is not much to expect of protoplasm, which shows a finer development of the power of internal

local differentation, for instance, in the asymmetrical growth of the wall. This power of the protoplasm might be exercised only by certain tissues or cells, as the "passage cells" of the endodermis, but probably it is by no means so restricted.

Further, the solution given out under pressure must be more concentrated than the water that enters to take its place. This does not mean, though, that if, for instance filtration is from the endodermis, the sap in the xylem must be more concentrated than the cell-sap in the cortex. For all the living cells from the root hair to the wood may cooperate as a unit, so that if the solution in the xylem is just enough stronger than the water *in the ground* to overcome the slight resistance to its passage offered by the intermediate tissues, all the physical requirements are satisfied. It is likewise absolutely unnecessary that the deeper cortical cells have more concentrated sap than the root hairs, in order to withdraw water from them; although it is usually the case that the turgor increases from the epidermis inward. When an epidermal cell has taken in all the water it can hold, the underlying cell has only to contain cell sap osmotically stronger than the ground water in order that a stream may pass through into it.

The energy which the cells exerting root pressure lose in the filtration of a part of their osmotically active matter is not (except, in part or in whole, in guttation and bleeding) a real loss to the plant. It is returned when the water and solute are separated by evaporation. So that when root-pressure raises the transpiration stream, just as when any other method—capillarity, suction, imbibition, etc.—is used, the ultimate source of energy is those rays from the sun that evaporate the water. In extreme cases root pressure amounts to an atmosphere or so. The solute necessary to explain this will have no discernible effect upon the amount of transpiration, being too insignificant beside the energy always used in evaporation, which is sufficient at ordinary temperatures to lift the mass of water evaporated, without any change in its condition, about 140 miles.—

4. The self-registration of photosynthesis.

The employment of the graphic method has proved an invaluable aid in many fields of physiological research, and has at the same time been of even more general, if of less intense, utility as a feature of class demonstration. The very simple device described here, by which the method is extended to the new field of photosynthesis,

appeals at first sight to its availability for popular demonstration. Even for purposes of investigation it is free from most of the objections to the bubble-counting method, and subject only to such as necessarily attend work on water plants.

Submerged plants of some kind are fastened where the oxygen they set free as gas is collected under an areometer. They may be fastened

FIG. 2.[1]

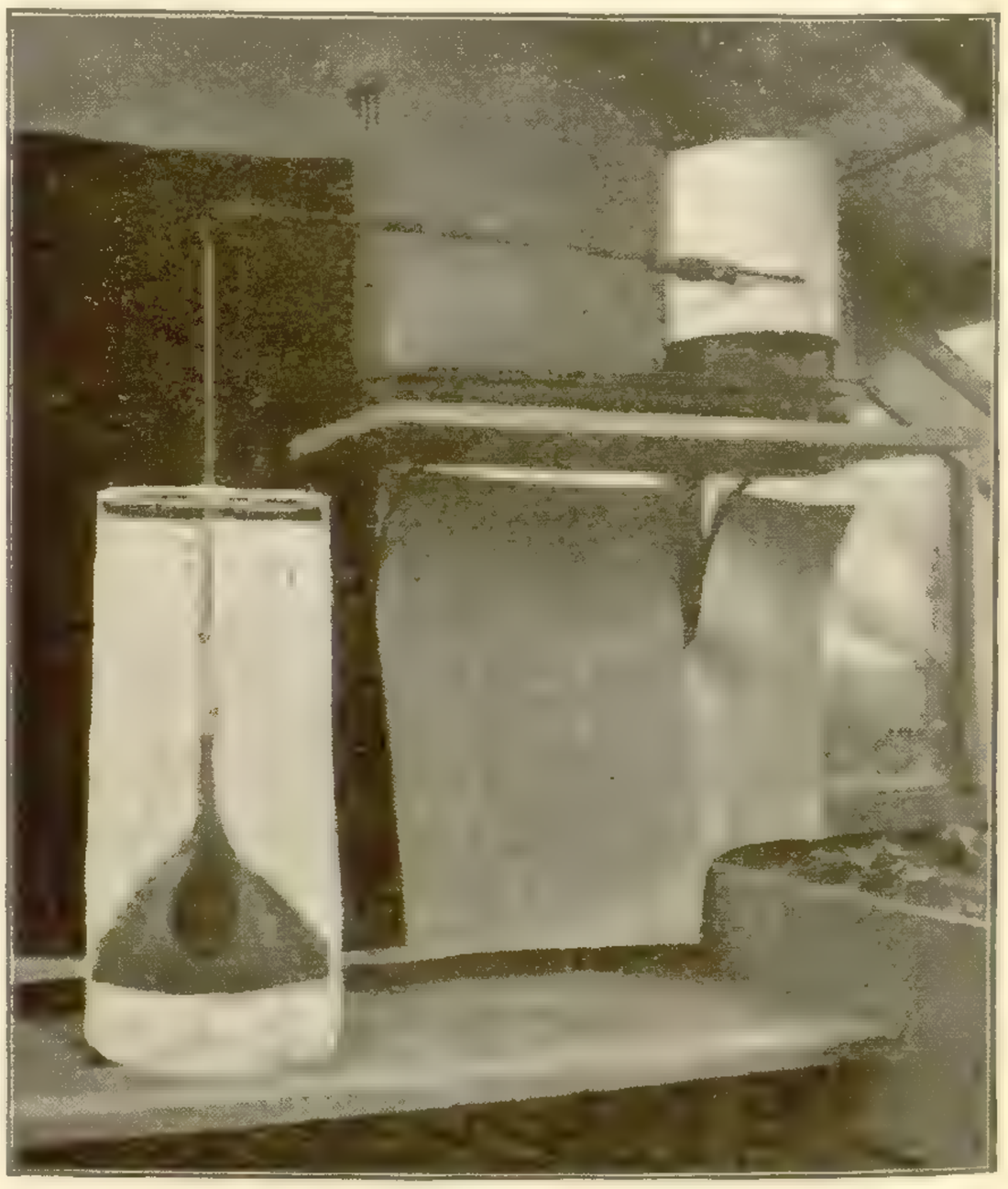


FIG. 3.

into a funnel, whose upper end is sealed into a tube of uniform external diameter, closed at the top (*fig.* 2). Or they may merely be tied into a beaker, or any other vessel, which is inverted and hung by a uniform rod. Because it is allowed to contain air, or preferably as it is held up by a counterpoise, this funnel or other vessel containing the plants stands with the uniform tube partly out of the water. As the plant assimilates, the oxygen set free displaces water, making lighter the vessel with its contents, which accordingly rises, lifting above the water a volume of the tube or rod equal to that of the oxygen evolved in the water below. It is indifferent whether the bubbles rise and

[1] Used by courtesy of the West Virginia Experiment Station.

collect in the tube or against the top of the beaker, as the larger ones do, or remain clinging to the leaves; or if only they displace water, they may stay within the tissues of the plant, and still make their record.

Of course having a rod whose upward movement shows the rapidity of the evolution of oxygen, it can very easily be made to leave its record; most accurately perhaps by means of the wheel described as the chief part of a "a new self-registering transpiration machine,"[2] but more conveniently sometimes, being less disturbed by drafts, by means of a lever auxanometer. One illustration shows it set up with a Corbett auxanometer (*fig. 2*); the other, with the wheel (*fig. 3*).

From a considerable bulk of green plant substance the evolution of oxygen is so rapid that it is necessary to use a rather large rod or get an inconveniently rapid drop of the tracer. With the auxanometer it is better to have the arms of the lever equally long. And with the wheel the tracer may be attached directly to the counterpoise, thus using only one wheel. I have tried the apparatus with Elodea and with Callitriche. The short record given here as an illustration of its work was obtained with Callitriche, May 10, beginning at 11:20 A. M., after a freezing night. The experiment was performed on the the roof, so that there were no shadows except from occasional clouds. The distance descended by the tracer and the indicated evolution of oxygen are both given. A change in weight of 1 ^{gm}, by the evolution of 1 ^{cc} of oxygen, caused the tracer to fall 17.7 ^{mm}. The registration was on a cylinder revolving in 20 minutes, but for the sake of brevity the record is condensed into one hour intervals. The temperature at 11 A. M. was 19°C.; at 1 P. M., 23°; and at 7 P. M., 21°.

	11:20–12	12–1	1–2	2–3	3–4	4–5	5–6	6–7	6:40–7
mm.	6.8	14.8	28.7	32.2	37.8	31.8	21.0	11.2	1.7
cc.O.	0.37	0.84	1.62	1.82	2.14	1.80	1.19	0.63	0.096

With the same plants on another day it was found that at 31° the evolution of oxygen was above 3 ^{cc} per hr., while at 36.4° it was only about 1 ^{cc} in the same interval. The explanation must be sought largely in the decrease in available CO_2 at the higher temperature.—Edwin B. Copeland, *University of West Virginia, Morgantown.*

[2] Bot. Gaz. **26**:343. 1898.

CURRENT LITERATURE.

BOOK REVIEWS.

Pfeffer's Physiology.

ALMOST as soon as the German edition of this great work appeared, announcement was made that it would be translated into English by Professor Ewart. The two years that have elapsed since the German edition was published have only whetted the desire of English-speaking students to have the work in a more familiar tongue, because they have found out how intricate and obscure the style of the original is. There is no need to speak again of the contents or value of the work itself.[1] Use of it has amply justified the enthusiastic reception with which it was greeted by students everywhere. Doubly welcome, therefore, is the elegant volume now before us, faultless from the bookmaker's point of view. One must pay for such elegance, however, and we would that the English edition had been kept down to the price of the German, instead of the almost prohibitive $7.00. The necessity of having both — German for what Pfeffer says and English for what Ewart says he says — makes the high price the greater burden.

For when one compares the English text with the original he is immediately impressed by the fact that this is not a translation in the usual sense. Indeed, the translator says in his preface: "The difficulty of the original German has necessitated the exercise of a certain freedom in the process of translation, but an exact interpretation of the original has been given throughout." No one could expect a literal translation of the original, and we are grateful that a free rendering in smooth idiomatic English has been made. While we here acknowledge to the full the indebtedness of students to Dr. Ewart for time and labor which he has expended to put before them this English version, it will not be considered ungracious, if for the benefit of users we raise the question whether it was necessary to take as many liberties with the text as the translator has done. These consist in the addition, omission, and alteration of qualifying words and phrases, to such an extent as often to make it questionable whether or not a given passage is "an exact interpretation of the original." Forewarned of this freedom of interpretation, it will be necessary for one to refer to the German text to determine for himself precisely what Pfeffer says, for it is these very qualifications which restrict or color his statements. Specific cases might be cited in almost unlimited number, were it not easy for anyone who cares to verify the statement to find

[1] See BOT. GAZ. **25**: 132. 1898.

numerous illustrations. The opening paragraph of § 49 may be taken as a fair example of general "interpretation." For instances of alteration take these two: "unvollkommenen Bundeln" of mosses (p. 197) is rendered "rudimentary vascular bundles (p. 216). Pfeffer would probably deny the morphological implication in the latter phrase; at least he had avoided it in his use of the original adjective. Again: "nachweisbaren Producten" of photosynthesis (p. 299) are not necessarily "visible products" (p. 317), and the change makes the sentence untrue. Nor will it be fair to consider the passage of the English proofs through Pfeffer's hands as equivalent to an endorsement of the translator's particular modes of expression.

The comparison with the original is necessitated further by the avowed changes which Dr. Ewart has wisely introduced. In the main these are indicated by brackets, but this should have been uniformly done. The later literature is cited and other betterments are noticeable. The avoidance of new terms is desirable whenever it does not involve too great circumlocution, and the new book has practically none. We note, however, the increased use of photosynthesis, which is making its way in spite of conservatism, though it is not used consistently. Ewart is in error regarding the term photosyntax (footnote, p. 302), which he rejects as unnecessary. It was defined by the proponent precisely as photosynthesis (p. 292), and could by no means include "all cases of carbon dioxide assimilation."

Some of the slips of the German text have been corrected, but two notable ones in § 40 have been missed. On p. 250 the amount of water transpired under favorable conditions is given as 1 to 10^{cc} per 24 hours "from a single square *centimeter* of leaf surface." This should read decimeter, the amounts named being 100 times too large. On p. 251 also the last two sentences of the middle paragraph should be transposed, the last one being meaningless in its present position.

Inasmuch as the cross-references are to sections it would have been convenient to have the section numbers in the page head, as in the German book. This disadvantage is much more than balanced, however, by the very complete index, an essential feature absent from the original.

The second volume is awaited with the greatest interest, and we trust the English version will appear promptly as promised. And we must not allow any differences of opinion or defects in the translation to mimfy our obligations to Professor Ewart and to the Clarendon Press for the helpful and elegant volumes.—C. R. B.

NOTES FOR STUDENTS.

Dr. J. Loeb has begun the publication of a series of articles containing new facts and ideas concerning the constitution of living matter, to which the attention of botanists should be directed. The first one,[2] on the poisonous

[2] Am. Jour. Physiol. 3: 327–338. 1900.

character of a pure NaCl solution, points out that the salts or electrolyte in general do not exist exclusively as such in living tissues but are ionized, and these ions are united with the proteids. "The great importance of these ion-proteid compounds lies in the fact that by the substitution of one ion for another the physical properties of the proteid compounds change. This accords with Dr. Loeb's own results on variable absorption of water by muscle, according as Na, K, or Ca ions were present, and explains some facts regarding the effects of salts upon turgor in plants. Loeb found pure NaCl solutions of equimolecular strength with sea water poisonous to Fundulus, a fish which can endure a great increase in the concentration of sea water, even an addition to it of 5 per cent. NaCl, while in distilled water young fish lived indefinitely. (True had previously shown that NaCl and KNO_3 are poisonous to Spirogyra.) He also found the medusa of Gonionemus non-contractile in NaCl, and was able to control its contractility at will by varying the solutions; ciliary movement and development in young larvae of the sea urchin could be modified in the same way. Loeb's conception as to the relation of metal ions to proteids and the protoplasmic functions suggests reexamination of the conclusions as to the elements necessary to the healthy development of plants. These conclusions have been based chiefly on the use of nutritive solutions from which certain salts were successively omitted. One element, however, may only be necessary to antagonize the action of another.—C. R. B.

THE FOURTH PAPER in Professor F. O. Bower's series entitled "Studies in the morphology of spore-producing members," deals with the leptosporangiate ferns.[3] The preceding papers dealt with Equisetineæ and Lycopodineæ (published in 1894), Ophioglossaceæ (in 1896), and Marattiaceæ (in 1897). The importance of the present contribution, dealing with the greatest of the pteriodphyte groups, can hardly be overestimated. In our limited space it is impossible to note a tithe of the interesting observations and suggestions. It will be remembered that Professor Bower excludes both Isoetes and Ophioglossaceæ from the Filicales, and in the present paper he only considers the homosporous forms. As thus limited, he proposes the three following great divisions of homosporous Filicales, which he calls suborders: *Simplices*, *Gradatae*, and *Mixtae*.

It may serve to a better understanding of the characters upon which these divisions are established to indicate the groups which they include. The *Simplices* include Marattiaceæ, Osmundaceæ, Schizæaceæ, Gleicheniaceæ, and Matonineæ; the *Gradatae* include Loxsomaceæ, Hymenophyllaceæ, Cyatheaceæ, Dicksonieæ (exclusive of Patania, Woodsia, Hypoderris, and Deparia), and Dennstaedtiinae; the *Mixtae* include Davallieæ (exclusive of

[3] Phil. Trans. Roy. Soc. B. **192**: 29–138. *pls.* 2 7. 1899. London: Dulau & Co., 37 Soho Square, W. 8*s*.

Microlepia), Lindsayeæ, Pterideæ, and other Polypodiaceæ, together with Woodsia, Hypoderris, and Deparia.

It is noted with interest and approbation that the terms Eusporangiatae and Leptosporangiatae are dropped as designating systematic divisions, but retained as descriptive words. The difference in the mode of origin implied by these terms is regarded as marking no important biological feature, whereas the distinction between the three groups proposed rests upon facts of far-reaching biological significance, and conveys in each case a definite morphological conception.

In the *Simplices* the sporangia are of simultaneous origin, upon a receptacle which may be slightly sunken, flat, or slightly projecting; also, they are of relatively large size, sessile, and usually produce a large output of spores (ranging from 128 to over 7000). The annulus when present is oblique, and dehiscence is in a median plane, correlated with freedom for lateral spreading. The protective arrangements are usually absent or inefficient, and the whole group is to be regarded as displaying primitive characters.

In the *Gradatae* the sporangia are borne in basipetal succession, with regular orientation, upon a more or less elongated receptacle; also they are usually of smaller size, sessile or with short stalks, and the output of spores is typically sixty-four or lower. The dehiscence is lateral and oblique; and the annulus is oblique, correlated with freedom only in a direction obliquely upwards. In general the indusium is present as a basal cup or basal flaps.

In the *Mixtae* the sporangia are of various ages intermixed, without regular orientation, upon a sunken, flat, or slightly projecting receptacle; also they are relatively small, with more or less elongated and thin stalks, and the output of spores is sixty-four or under. The annulus is vertical, and the dehiscence transverse, correlated with freedom directly upwards. The protective arrangements are various, and often elaborate.

These three divisions the author regards as illustrating the three steps in the evolution of the sporophyte in homosporous Filicales. He does not suggest a single line of descent, but rather parallel development, the members of each of the three divisions not necessarily being of common descent, but grouped according to common adaptation, just as are the seed-plants.

It would be profitable to consider the summaries of information given under each group; also the morphological discussion of the sorus, including the indusium, the receptacle, and the sporangium with its stalk, annulus, and output of spores; and also the discussion of the biology of the sorus, which includes the production and nutrition of spores, their protection till maturity, and their dispersion; but for all these interesting topics the original paper must be consulted.—J. M. C.

Mr. W. A. Cannon has published the results of a morphological study of the flower and embryo of *Avena fatua*, the wild oat (Proc. Calif. Acad.

III. 1 : 329–364. *pls.* 5. 1900.) The investigation of some of the grasses from the modern morphological standpoint has long been a *desideratum*, as they have had the reputation of being exceptional in certain features, and because of the question as to their primitive or reduced character. The author states his results in a remarkably clear and well organized summary, from which certain points bearing upon mooted questions may be noted. The lodicules are regarded as stipular rather than "perianthal;" the earlier growth of the stamen is mainly intercalary in the anther; the staminate archesporium is composed of a single row of cells, and each spore mother cell touches the tapetum; the wall of the microsporangium consists of tapetum, middle layer, and endothecium; the generative nucleus divides in the pollen grain, and the male cells are elongated spindle-shaped; the archesporial cell of the ovule cuts off no tapetum; the four potential megaspores are formed in various ways, (1) by four nuclei without cell walls, (2) by the development of four nuclei which later are separated by walls, (3) by the usual appearance of walls following each nuclear division, in which features there is a close resemblance to Eichhornia as investigated by R. Wilson Smith; the antipodals multiply before the fertilization of the egg, becoming thirty-six or more in number, and begin to disorganize with the beginning of endosperm development, apparently serving to nourish the forming endosperm, as that in turn nourishes the embryo; the endosperm first aggregates about the forming embryo, a fact which seems to be correlated with the feeble development of the suspensor, which consists of but a single cell; in its development the embryo of *Avena fatua* illustrates all three of the "types" of Nörner; the cotyledon and the stem-apex are derived from the distal segment, the root, the root-cap, and periblem initials of the root from the middle segment, and the coleorhiza from the basal segment; the organs of the embryo originate in the distichous manner characteristic of the vegetative leaves of grasses.

It is to be regretted that the author's material did not permit him to determine the fate of the second male cell, especially in a family in which the phenomenon of xenia occurs, which seems to be best explained as an evidence of double fertilization.—J. M. C.

DR. ARNOLD GRAF objects to the term cytology as far too general, and proposes the following subdivisions of the subject: cyto-morphology (external form and size); cyto-anatomy (organization); and cyto-physiology. The latter is further divided into *a*) cyto-mechanics (physical properties and behavior to mechanical stimuli), including cyto-statics (conditions of equilibrium) and cyto-dynamics (phenomena of motion, including cell-division maturation and fertilization, death and *pro parte* pathology); and *b*) cyto-chemistry.—C. R. B.

NEWS.

DR. JULIA W. SNOW has been appointed instructor in botany in Rockford College, Illinois.

MR. FREDERICK O. GROVER has been promoted to the professorship of botany in Oberlin College.

DR. RODNEY H. TRUE has been appointed lecturer in botany at Harvard University during the absence of Dr. George L. Goodale next year.

PROFESSOR JOHN BRETLAND FARMER, of the Royal College of Science of London, has been selected by the Royal Society for election to membership.

THE INTERNATIONAL ASSOCIATION for the Advancement of Science, Art, and Education will hold its first assembly in connection with the Paris Exposition. In the long list of congresses, that of botany is announced for October 1 to 6.

MR. CHARLES E. SMITH, one of the prominent botanists of Philadelphia, died recently. By his will the Philadelphia Academy of Natural Sciences receives his botanical library and herbarium, and one sixth of the estate, which is estimated at $500,000.

TWO SETS of Bailey's *Cyclopedia of American Horticulture* are being cut up and pasted on sheets in the economic herbarium of the Department of Agriculture. This will give a working list of *desiderata* for the cultivated plants of the United States.

THE LAST *Bulletin of the New York Botanical Garden* (1: [no. 5] 295–449. *pls. 10–12.* 1900) contains the various reports for 1899. From them we learn that during the year the herbarium received accessions of specimens to the number of 70,000; and that over 4000 species and varieties of plants are under cultivation in the various plantations, 172 families and 1057 genera being represented.

DR. B. M. DUGGAR, of Cornell University, has received the appointment from the Smithsonian Institution, to the research table at the Statione Zoölogica, Naples, Italy, and has already entered upon his work there. He has been in Europe during the past year, has visited England, Sweden, Germany, and Italy, and has been studying at Leipzig and Halle until his departure from the latter place for Naples. He expects to return to Cornell University in July.

THE FIRST ISSUE of the *Popular Science Monthly*, that for June, under the editorial management of Dr. J. McKeen Cattell has appeared. It gives promise of a strong grasp upon a very important constituency, one which is eager to read about science and is in peculiar danger of being imposed upon by science "falsely so-called." The editor and the long list of men of science who have promised to support the journal are a guarantee that the standard will be very high, and that the contents may be depended upon. In this number Professor D. T. McDougal has given an interesting and well-illustrated account of The New York Botanical Garden, and several botanical reviews appear.

IN THE *Journal of Botany* for June (pp. 224–229) there is reproduced an overlooked paper by Rafinesque. It is not included in Dr. R. E. Call's account of the *Life and Writings of Rafinesque*, is not in the Royal Society's *Catalogue of Scientific Papers*, and several names in the paper are not to be found in the *Index Kewensis*. It was published in Loudon's *Gardeners' Magazine*, nineteen volumes of which appeared (1826–1843). The title of the paper is "Remarks on the Encyclopædia of Plants of Loudon, Lindley, and Sowerby," and the citation is Loudon's *Gard. Mag.* 8: 245–248. 1832. The comments are in the usual style of Rafinesque, very brief but very direct, and it will be a matter of interest, as Dr. James Britten suggests, to collate the names with the *Kew Index* and with American nomenclature. The paper closes with the characteristic statement that "Botany will never be permanently fixed until all errors are exploded and corrected."

GENERAL INDEX.

The most important classified entries will be found under Contributors, Disease, Personals, Reviews, and Work. **New names, and names of new genera, species,** and varieties, are printed in **bold-face type**; synonyms in *italics*.

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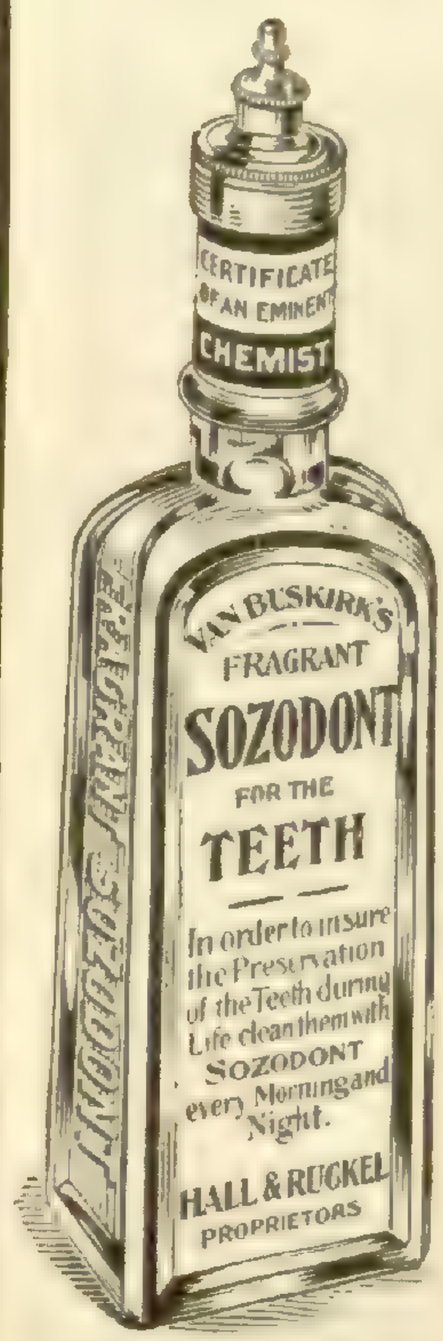

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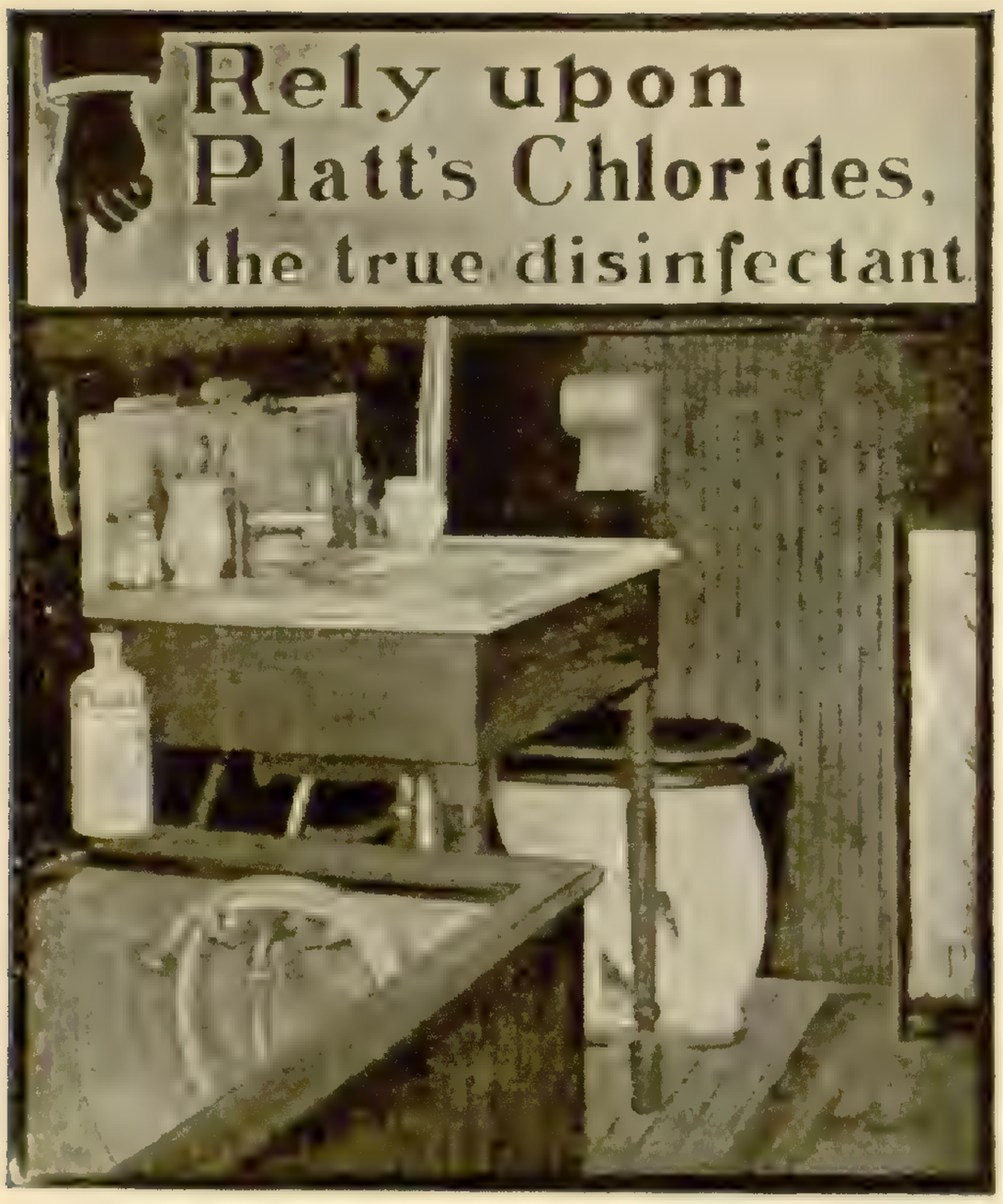

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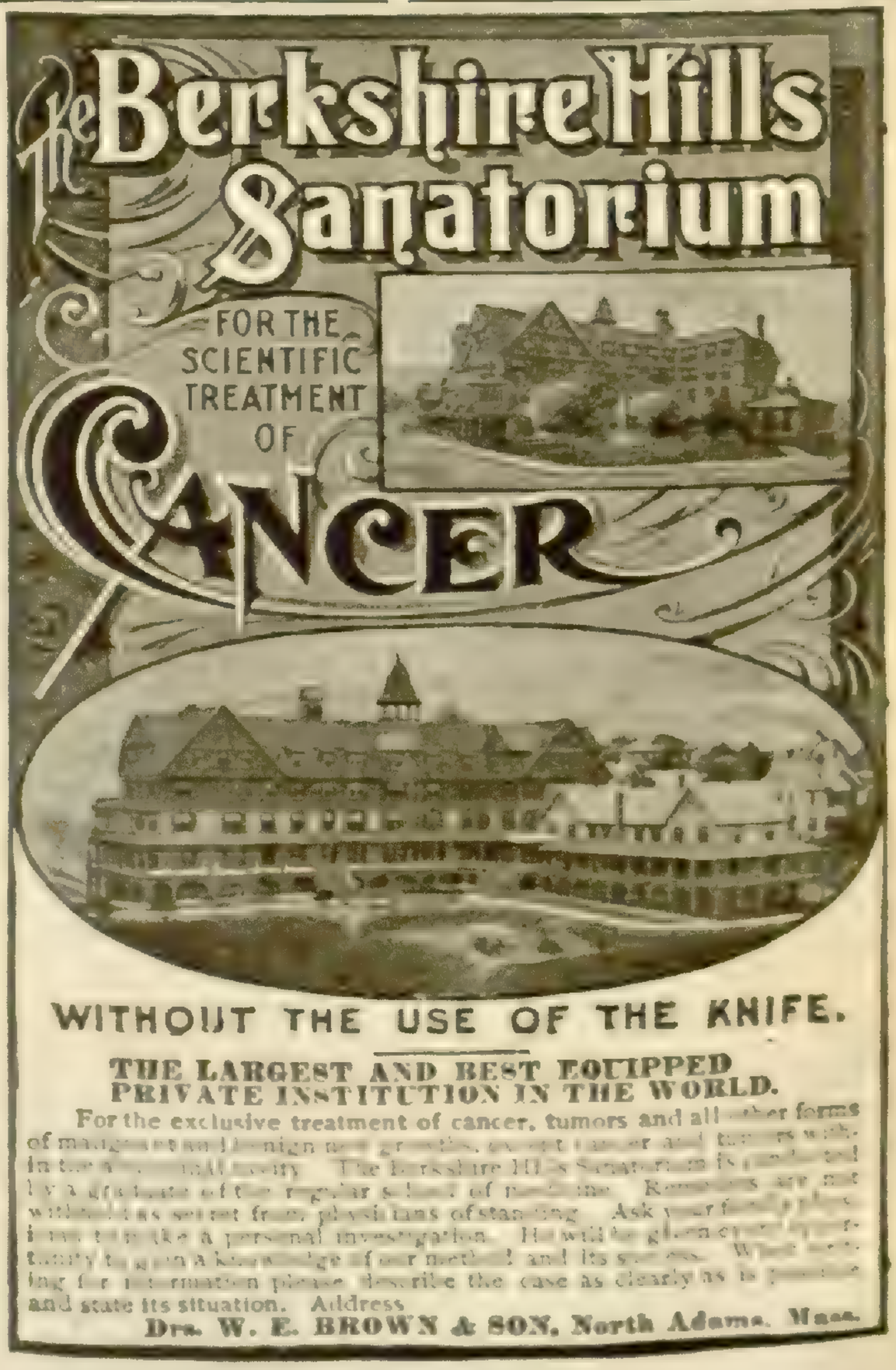
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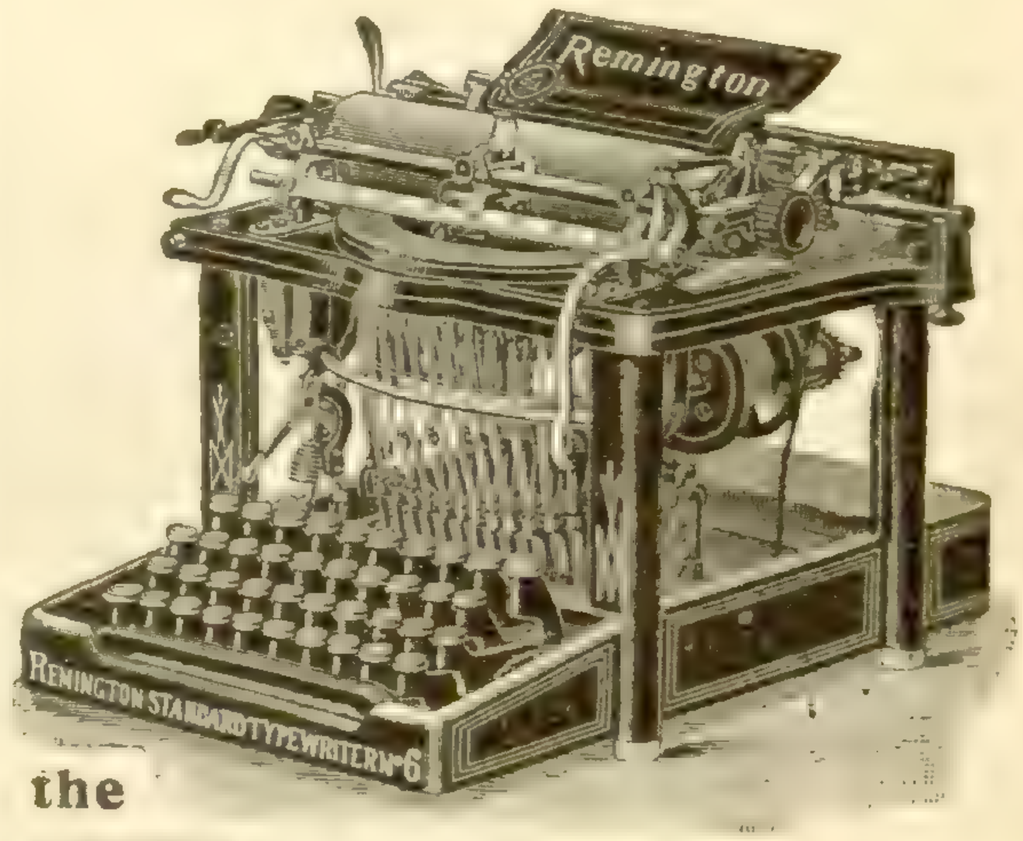

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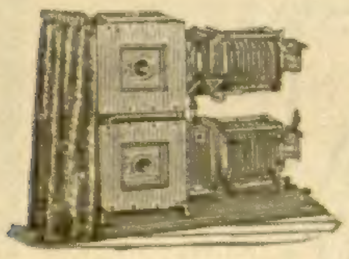

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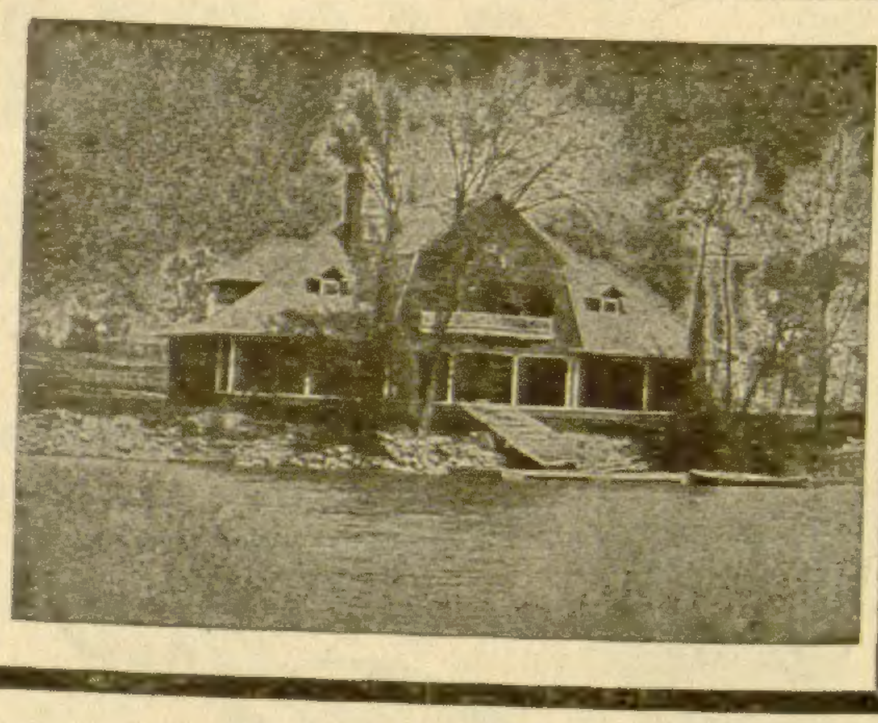

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